

## Structure and function of ant (Hymenoptera: Formicidae) brains: Strength in numbers

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### Abstract

This article reviews the brain of ants in the context of their behavior. Division of labor underlies the social lifestyle of ants; it results not only in behavioral specialization, but also in some adaptations of ant brains. The structure and function of major brain neuropils is described (visual and olfactory centers and central multi-sensory integrative brain compartments) together with some of their neurons. Unlike social vertebrates, which have larger brains and cerebral cortices than solitary species, ant brains are not bigger than those of solitary insects, but they are more specialized. The biological success of ants is probably not so much the result of an individual's brain as of the concerted action of a colony's hundreds or thousands of brains.

**Key words:** Social brain, neuroanatomy, neurophysiology, olfaction, vision, review.

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### Brains reflect the ants' behavior and environment

Ants are insects, and their brains conform to the general design of insect brains, just as human brains reflect their vertebrate, mammalian and primate origins (reviewed by STRIEDTER 2005). Before trying to understand the composition and function of ant brains we have to briefly recapitulate what is special about ants, and their behavior in particular.

Sociality should affect not only the behavior of ants, but also the brains that generate and control the behavior. In particular, the brain composition might reflect the behavioral specialization (division of labor), most notably between sexuals and worker castes. Chemical (pheromones) and mechanical communication (vibration, touch) among nestmates are hallmarks of a social lifestyle, and one might expect these sensory modalities and their neural substrate to be well developed in ants. Ant workers of all subfamilies are wingless and even the alate sexuals are poor fliers compared to wasps and bees. This obviously shapes the motor output (controlling leg instead of wing movements), but it also affects sensory input: flight relies predominantly on vision and also on information about air-currents, gravity and acceleration, all of which are much less important for terrestrial locomotion. Instead, the sense of touch will play a major role for ant locomotion.

For foragers, it is essential not only to locate food resources, but also to find their way back home. Trails may be marked by pheromones, but many ants rely on visual navigation (and probably olfactory and magnetic cues), as has been particularly well studied in *Cataglyphis* desert ants by Rüdiger Wehner and his colleagues (WEHNER 2003). Besides the perception of stimuli, this requires learning and memory abilities allowing ants to remember odors (ROCES 1994, DUPUY & al. 2006) or directions and make use of landmarks. Other kinds of learning are important for

nestmate recognition, and generally learning and memory are beneficial in novel or changing environments. One might therefore expect to find ant brains equipped with structures and mechanisms that allow advanced learning and memory to take place.

Among Hymenoptera, brain research has mainly focused on honey bees (*Apis mellifera*), which have become a model system for insect behavioral brain research. The bee brain has been well and accurately described anatomically more than a century ago by KENYON (1896), and all modern descriptions of ant brains refer to this standard. Historically, ant brains have been repeatedly examined and described since DUJARDIN (1850), but few studies have compared brains of different ant species (e.g., BURLING-THOMPSON 1913, PANDAZIS 1930). Much of what is known about ant brains has been done on larger ants (mainly workers), in particular larger *Camponotus* species, because brains are easier to dissect in larger insects. Size is even more important for physiological studies, and this is the reason why there are very few attempts to electrically record activity from and response properties of nerve cells (neurons) in ants (JUST & GRONENBERG 1999, RAMON & GRONENBERG 2005, YAMAGATA & al. 2005, 2006). Only two studies have attempted to measure brain activity using recent, advanced optical recording techniques (calcium imaging) in ants (GALIZIA & al. 1999, ZUBE & al. 2008). This review will therefore focus mainly on functional brain anatomy. If the function of particular brain components has not been established in ants, it will be inferred by homology with other Hymenopterans or insects (e.g., the optic lobes process visual information in any known insect).

Ant brains show all the characteristics and components one would expect to find in an insect brain (Fig. 1). The

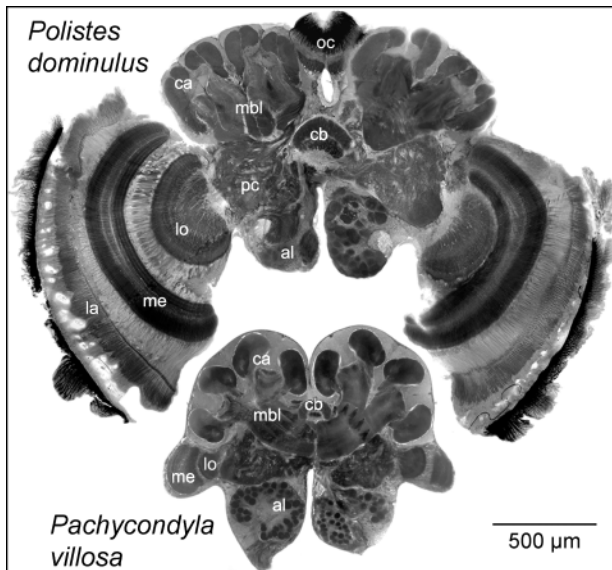


Fig. 1: Brain of a paperwasp *Polistes dominulus* (top) and worker of the ponerine ant *Pachycondyla villosa* (bottom); microtome sections (15 µm) of osmium-stained material; antennal lobe (al), mushroom body calyx (ca) and lobes (mbl), central body (cb), lamina (la), medulla (me), lobula (lo), protocerebral lobe (pc), median ocellus (oc).

major brain compartments are labeled in Figure 1 for a paper wasp (*Polistes dominulus*) and a relatively basal ant (*Pachycondyla villosa*) and will be discussed below: the optic lobes (visual centers) lamina, medulla and lobula (lamina not shown for the ant in Figure 1 because it often detaches from the brain during dissection); the primary olfactory center (antennal lobe), the protocerebral lobes, the central body, and the mushroom body, which comprises the calyx and the mushroom body lobes. In ants and other holometabolous insects, the subesophageal ganglion (Fig. 2a) is fused to the brain posteriorly. This ganglion is organized like a "typical" insect ganglion (e.g., thoracic ganglia) and is thus less complex than the brain proper and differs little among insects; it will therefore not be further considered in this review. While the sizes of the different brain components differ in ants and closely related vespid wasps (Fig. 1), the only structures that are absent in ants are the ocelli and their associated neurons as most ant workers do not have functional ocelli. Overall, the brain of *Pachycondyla* (Fig. 1) is typical for ants, although there are minor differences between subfamilies and between species with different ecological adaptations (e.g., visual predators vs. seed harvesters) and species (or castes) with small body or head size.

The most obvious difference between brains of wasps and ants is in the size of the optic lobes, which are very small in ants in general, although there are some exceptions (see below). In contrast, the antennal lobes and the protocerebrum and its components appear similar in size compared to the wasp brain (Fig. 1). There is also a pronounced difference in overall brain size across ants; however, as brain size in all animals (JERISON 1973), including ants (WEHNER & al. 2007), generally correlates with body size, one would expect the ant to have a smaller brain than the larger paper wasp.

## The sense of smell and olfactory processing

Insect antennae are appendages that carry many sensilla that sense mechanical stimuli (touch, vibrations) and, in almost all advanced insects, and in ants in particular, odor stimuli. Other antennal sensilla perceive stimulus modalities different from "ordinary" odors: some respond to chemical stimuli that one would refer to as taste, e.g., salty, bitter or sweet substances; hygrometers respond to humidity, thermoreceptors signal temperature changes, and specialized receptors inform the ant about the concentration of carbon dioxide (KLEINEIDAM & al. 2000). All these sensilla are hair-like structures or modified and derived from hair-like structures and contain one or more sensory neurons. The majority of sensilla on the antenna contain olfactory neurons that respond to particular subsets of odors or chemical compounds.

Importantly, antennae are extremities that can be moved around to scan a larger volume of air or to probe structures, crevices, trails or other insects including nestmates for chemical and tactile cues. To perform antennal movements, antennae are equipped with sets of muscles inside the head capsule and others inside the antenna's basal segment, the scape. All of these muscles are controlled by motor neurons that reside in a brain region behind (posterior to) the antennal lobe, referred to as dorsal lobe. This part of the brain also receives mechanosensory input from the antenna (EHMER & GRONENBERG 1997), hence antennal movement and the tactile input resulting from that movement can be integrated together by the dorsal lobe.

Each olfactory receptor neuron (c. 50,000 - 60,000 in *Formica pratensis*, GOLL 1967) in the antenna sends an axon, a long nerve fiber, through the antennal nerve into the antennal lobe of the brain, where the axons terminate on and interact with secondary neurons (interneurons). Antennal lobes are particularly large in ants for two reasons: firstly, ants strongly rely on olfaction, more so than many other insects (which have more elaborate visual behaviors); and secondly, pheromone communication is most advanced and elaborate in ants compared to any other group of social insects (let alone solitary insects). The antennal lobes process both, "ordinary" odors and pheromones. Olfactory axons terminate in the antennal lobe in globular structures, called glomeruli (Fig. 2b). The sensory neurons supplying the glomeruli can be traced by mass-filling the antennal nerve, which reveals all the glomeruli (Fig. 2b).

Homology with *Drosophila* suggests that each glomerulus receives input from only one particular kind of sensory neuron (but many individual neurons of that kind) which in turn expresses one specific kind of odor receptor molecule at their receptive site in the antennal sensillum. Thus, one antennal lobe glomerulus might correspond to one particular kind of odorant receptor molecule and recognize a subset of odor molecules out of an almost infinite number of chemical compounds (VOSSHALL & al. 2000; reviewed for insects and vertebrates by KORSCHING 2001). The sensitivity and specificity of olfactory sensory neurons may vary (DUMPERT 1972).

This arrangement between sensory neurons and antennal lobe glomeruli suggests that, in general, the number of glomeruli in an insect correlates with the number of odors that can be discriminated, or with the precision that odors can be distinguished. While few studies have compared the number of glomeruli across taxa, it appears that

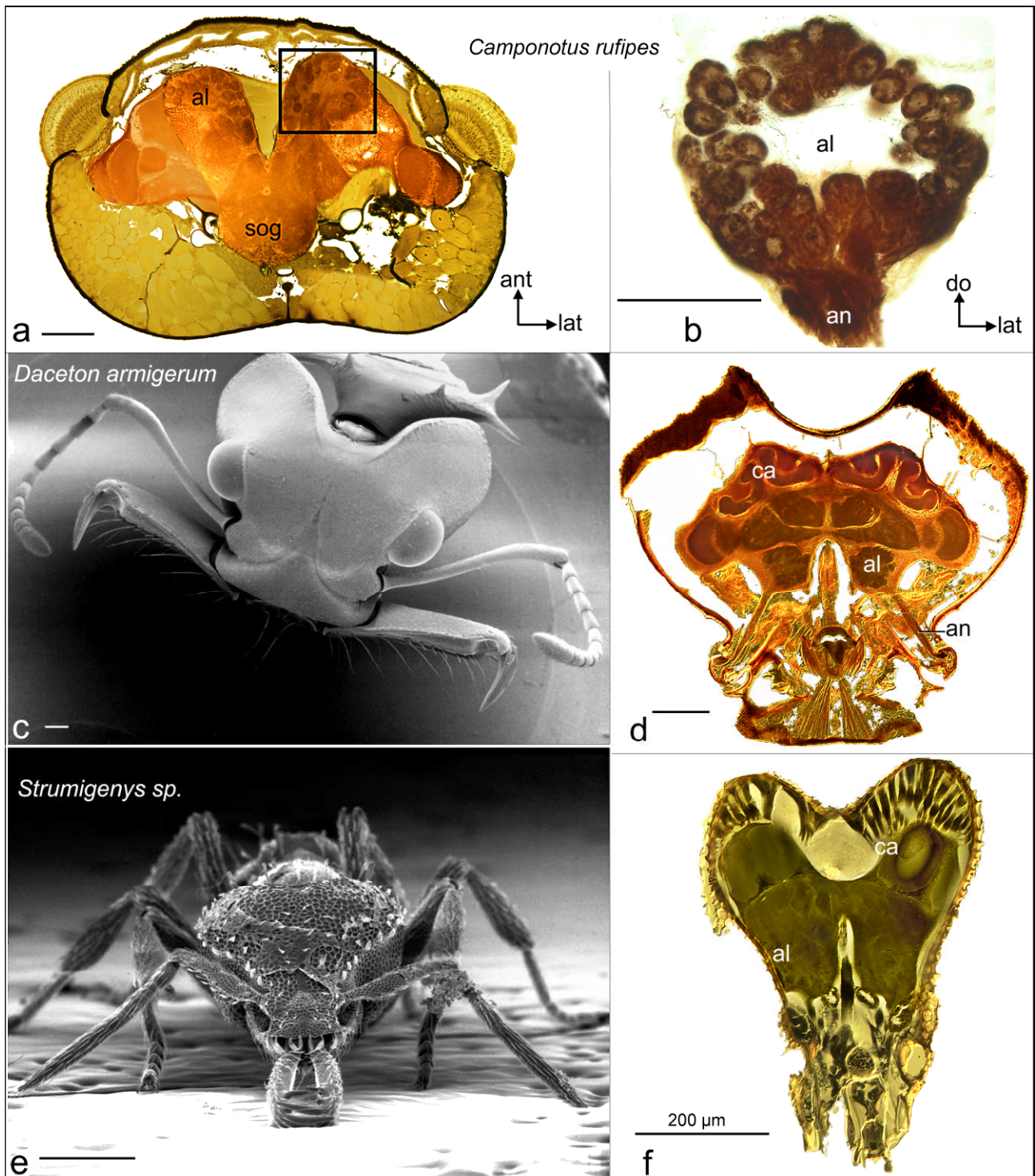


Fig. 2: Heads, brains and antennal lobes of workers of the formicine ant *Camponotus rufipes* (a, b) and the dacetine ants *Daceton armigerum* (c, d) and *Strumigenys* sp. (e, f); horizontal (a) and frontal (vertical) sections (b - f); reduced silver (a, d), osmium (f) and cobalt chloride stain (b). Areas boxed in a enlarged in b. Antennal lobe (al), antennal nerve (an), mushroom body calyx (ca), subesophageal ganglion (sog), directions anterior (ant), dorsal (do), and lateral (lat). Scale bars = 200  $\mu$ m.

ants may have a particularly high number of glomeruli (c. 430 in *Camponotus japonicus*, NISHIKAWA & al. in press;  $415 \pm 14$  in *Camponotus floridanus*, ZUBE & al. 2008; c. 200 in *Formica pratensis*, GOLL 1967). This compares to smaller numbers established for other insects: 43 in the fruit fly *Drosophila melanogaster* (STOCKER 1994),

63 in the Sphinx moth *Manduca sexta* (ROSPARS & HILDEBRAND 2000), 109 in the cockroach *Blaberus craniifer* (CHAMBILLE & al. 1980), and c. 160 in honey bee workers (FLANAGAN & MERCER 1989). Body size does not seem to be much correlated with the number of glomeruli: the small ant *Strumigenys* sp. (Figs. 2e, f) has considerably

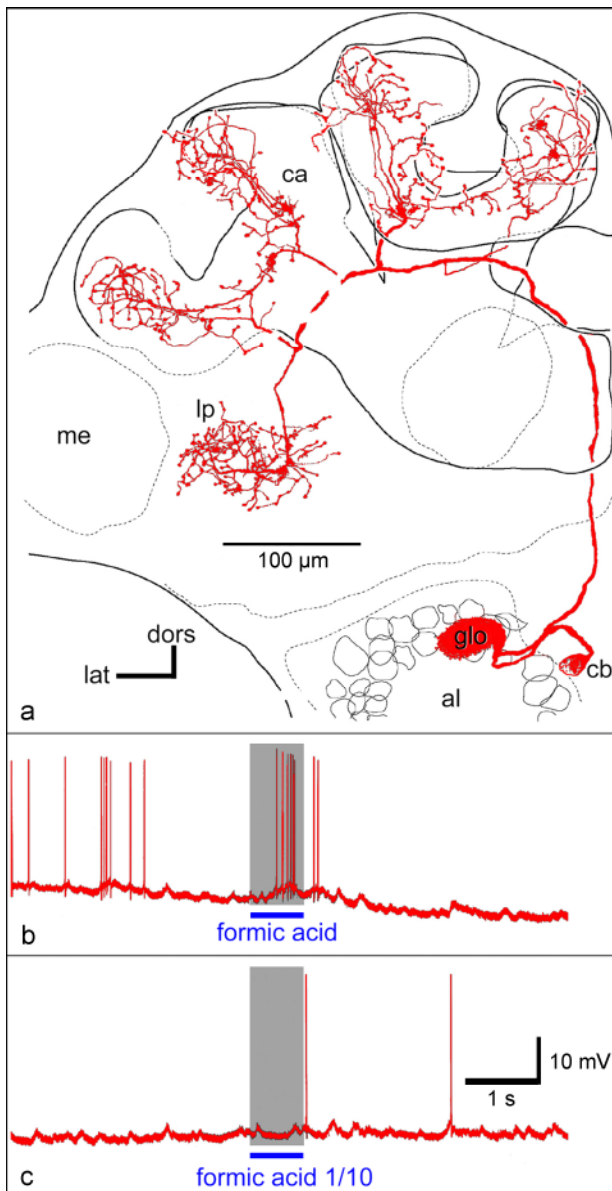


Fig. 3: Olfactory projection neuron recorded from and stained in the brain of a carpenter ant (a). It receives input in a single large glomerulus (*glo*) in the antennal lobe (*al*) and projects (sends output) to the mushroom body calyx (*ca*) and the lateral protocerebrum (*lp*). It responds to the alarm pheromone component formic acid (stimulus duration: blue bar) at higher (b) and lower concentrations (c), suggesting that the large glomerulus in (a) processes alarm pheromone information. Medulla (*me*); modified after YAMAGATA & al. (2006).

more glomeruli (c. 220) than the larger (and socially more advanced) ant *Daceton armigerum* (c. 120 glomeruli, Figs. 2c, d).

Information provided to the individual glomeruli from the odor receptor neurons on the antenna is integrated by local interneurons in the antennal lobe. These neurons are called "local" because their processes (input and output branches) are restricted to the antennal lobe. Many local interneurons have inhibitory responses and are supposed to sharpen the contrast of the perceived odorants (HILDE-

BRAND & SHEPHERD 1997). Olfactory information processed by the antennal lobe is transferred to "higher" brain centers [the mushroom bodies (see below) and the lateral protocerebrum] by projection neurons (Fig. 3), which interact with single or multiple glomeruli. Information about complex odor mixtures, concentrations and temporal properties of odor plumes is assumed to be coded by the simultaneous activity of many parallel projection neurons and the correlation and synchronicity of their action potentials [the smallest units of information in nerve fibers, in a way comparable to the binary digits (bits) in a computer line]. Properties of olfactory projection neurons have been described in other insects (reviewed by HANSSON 2002) and recently in carpenter ants (Fig. 3, YAMAGATA & al. 2006).

Much is known about pheromone communication in ants regarding the behavior, the glands and the chemical compounds involved (reviewed in HÖLLDOBLER & WILSON 1990), but little research has been done on the neural processing of pheromone information. In principle the perception and processing of pheromone information does not differ much from that of other odorants. Many insects have specialized glomeruli that process the different components of sex pheromones; usually, the number of specialized glomeruli reflects the number of chemical compounds that constitute the pheromone blend (reviewed for insects by HANSSON 2002). This has recently also been shown for carpenter ants (NISHIKAWA & al. in press). Different castes have different thresholds for particular odorants (LOPEZ-RIQUELME & al. 2006), which probably results from differences in the number of receptor neurons for particular odorants. However, it also results in differences in the central processing: a glomerulus that receives fewer input neurons from the antenna will be smaller than one that receives more input neurons. Thus two species of leafcutting ants that differ in their sensitivity to particular trail pheromone compounds also differ in the size of the respective assumed pheromone sensitive glomeruli (KLEINEIDAM & al. 2005).

Nest odors are used as recognition cues for nestmates and in that respect they are similar to pheromones. They are colony-specific complex mixtures of cuticular hydrocarbons, and like multi-component pheromones they have to be decoded by the olfactory system. It is unlikely that particular neuronal specializations are required to analyze nest odors – the task does not seem much different from analyzing the complex bouquets of odorants emanating from food items.

#### Ant vision: from nonexistent to highly acute

Ants in general are not particularly visual animals. This is reflected by the small size or even absence of eyes in many ant species that rely on tactile and chemosensory orientation. The extinct primitive ant genus *Sphecomyrma* and extant basal genera *Nothomyrmecia* and *Myrmecia* have relatively large eyes, suggesting that these predators rely on vision, as do some more advanced genera in different subfamilies (e.g., *Harpegnathos*, *Gigantiops*, *Myrmoteras* and *Pseudomyrmecinae* genera).

Like other insects, male and female ants have three ocelli (simple eyes, Figs. 4b, c), but most ant workers do not have ocelli (Fig. 4a, exceptions are pronouncedly visual ant genera such as *Myrmecia*, *Harpegnathos* and *Gigantiops*). More important are the compound eyes, which are

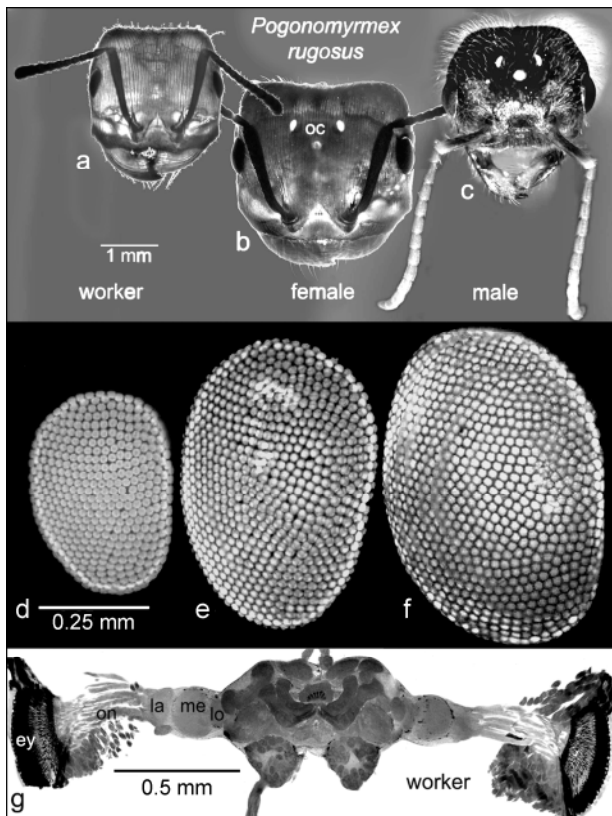


Fig. 4: Heads (a - c), eyes (d - f) and brain (g) of the seed harvester ant *Pogonomyrmex rugosus*: worker (a, d, g), female (b, e) and male (c, f). Note that workers have no ocelli (oc). Compound eye (ey), lamina (la), lobula (lo), medulla (me).

composed of many facets or ommatidia, each of which acts like a simple eye and comprises a lens and set of photoreceptors and supporting cells. Each ommatidium resolves only a single point in space, hence the more ommatidia an eye has, the better is its spatial resolution. Ommatidia number and spatial resolution are high in workers of the visual predators mentioned above (*Gigantiops* c. 4100 ommatidia, *Myrmecia* c. 3200 ommatidia, *Harpegnathos*, c. 1600 ommatidia) and in males and females of many ant species (e.g., *Ectatomma* male c. 1400, *Myrmiarium* male c. 1500 ommatidia, GRONENBERG & HÖLLDOBLER 1999). Figures 4d - f show the caste differences in eye size for *Pogonomyrmex* harvester ants (worker: 395, female: 640, male: 803 ommatidia), which is typical for many ants.

Within a species, eye size and ommatidia number depend on body (or head) size. KLOTZ & al. (1992) describe c. 375 ommatidia for small workers (head width 1.2 mm) and 658 ommatidia for large workers (head width 3.5 mm) of *Camponotus pennsylvanicus*. MENZEL & WEHNER (1970) showed similar correlation of ommatidia number with body size for the desert ant *Cataglyphis bicolor*, where the larger ants with more (c. 1200) ommatidia showed better visual orientation abilities (WEHNER & MENZEL 1969) and served as foragers whereas the smaller workers (c. 600 ommatidia) stayed inside the nest. Remarkable adaptations of ommatidial size to match a species' respective preferred light conditions (diurnal vs. nocturnal) have recently been shown for different *Myrmecia* species (GREINER & al. 2007).

Despite the modest visual capabilities of ants in general, even ants with small eyes (e.g., *Leptothorax albipennis*; 60 ommatidia) are able to use bold landmarks as beacons (MCLEMAN & al. 2002).

Photoreceptors can differ in their spectral sensitivity, which enables most advanced insects to discriminate colors. Ants were the first insects shown to perceive ultraviolet light (LUBBOCK 1881) and color vision has been behaviorally shown for a few ant species (e.g., *Formica*, *Cataglyphis*, KIEPENHEUER 1971, KRETZ 1979). However, in the majority of ant species color vision is probably not as advanced as it is in most other Hymenoptera as ants appear to have only two photopigments (*Myrmecia*: LIEKE 1981, *Cataglyphis*: MOTE & WEHNER 1980, *Formica*: MENZEL & KNAUT 1973) while most bees and wasps have three (reviewed by BRISCOE & CHITTKA 2001). A behavioral study in the highly visual ant *Cataglyphis* suggested the presence of three photopigments (KRETZ 1979), but these findings have not been reconciled with the physiological data. A study in the leafcutting ant *Atta sexdens* suggests only a single type of photopigment, which would render leafcutting ants color blind (MARTINOYA & al. 1975). This might also be true for many other ants that are either nocturnal or depend less on vision than do *Myrmecia*, *Cataglyphis* and *Formica*.

Besides color, the brain of ants probably processes information about motion, patterns, directions (position of the sun, polarization pattern of the skylight) and landmarks. The only aspect of vision that has been well studied in ants is visual orientation, and in particular polarization vision, mainly in *Cataglyphis* desert ants by Rüdiger Wehner and his collaborators (reviews: WEHNER 1994, 2003). Polarization vision is based on the polarization sensitivity of particular photoreceptors in the dorsal rim area of the eye. The processing of polarization information by central brain components has been worked out in locusts (HOMBERG 2004), but not in ants.

Almost nothing is known about central visual information processing in ants – no neurophysiological data exist on visual interneurons in ants. However, anatomical similarity suggests that basic processing mechanisms are similar in ants (EHMER & GRONENBERG 2004) and other holometabolous insects, except that processing will be less sophisticated in most ants, as indicated by their much smaller eyes and optic lobes (central visual processing centers).

Photoreceptors send their axons from the compound eye through an optic nerve (or often a loose bundle of parallel nerves, Figs. 4g, 5a) to the brain. Most photoreceptor axons terminate in the first optic ganglion (the lamina, Fig. 5a). A striking feature of the optic lobes is their precise and orderly design. They are arranged in a retinotopic way: information originating from one ommatidium in the eye and representing a particular point in visual space is processed by a particular array of neurons arranged in a "cartridge" in the lamina and a corresponding "column" in the downstream optic ganglia medulla and distal parts of the lobula, such that a point in space is processed by analogous and interconnected sets of neurons in the retina (ommatidium), lamina, medulla and lobula (reviewed by STRAUSFELD 1989). Some of these parallel fibers can be seen in the silver-stained preparations in Figures 5b, c. Visual processing in the insect lamina is assumed (STRAUSFELD 1989) to underlie phenomena such as adaptation in response to

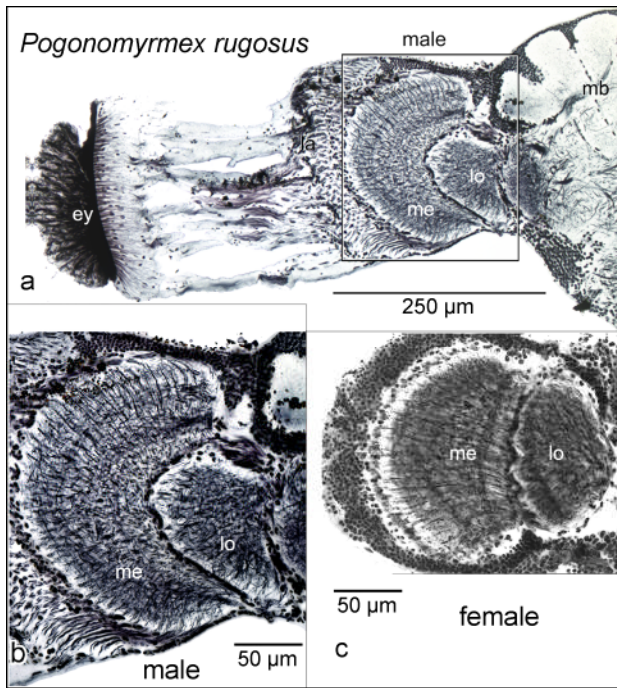


Fig. 5: Brain and optic lobes of the harvester ant *Pogonomyrmex rugosus*. Males (a, b) have larger optic lobes than workers (c). Bodian stained sections show the regular (retinotopic) arrangement of fibers in particular in the outer medulla. Area boxed in (a) is enlarged in (b) and (c). Antennal lobe (*al*), compound eye (*ey*), lamina (*la*), lobula (*lo*), medulla (*me*), mushroom body (*mb*).

changing light intensities, summation (which increases light sensitivity but reduces spatial resolution), enhancement of signal-to-noise ratio, and lateral inhibition (which locally enhances the contrast of the perceived image). Lamina neurons proceed to the medulla, where they contact many different classes of local interneurons (STRAUSFELD 1976) as well as lateral (tangential) neurons that connect several medulla "columns" and thus process information across points in space. Both types of neurons can be seen in the medulla of male and female harvester ants (Figs. 5b, c). One of the many functions of the medulla is to process color information. A second and parallel function of the medulla probably is to extract motion information from the visual input, in particular local or small-field motion events. However, the large number of types of neurons comprising the medulla, as well as its size (it is the largest of the optic lobes) suggests that it is involved in many different and complex kinds of visual processing (reviewed by STRAUSFELD 1989).

The retinotopic organization is rendered more coarsely in the third optic ganglion, the lobula, where each column now integrates information originating from several ommatidia, or sampling points (STRAUSFELD 1989). In the lobula, wide-field neurons integrate motion information over large parts of the visual field. Such wide-field or panoramic motion is important for an animal's movement control in space and has been intensively studied in flies (reviewed by BORST & HAAG 2002). The lobula comprises large- and small-field neurons and probably represents both, color and motion information, but otherwise little is known about the kinds of information processing performed in the lobula or

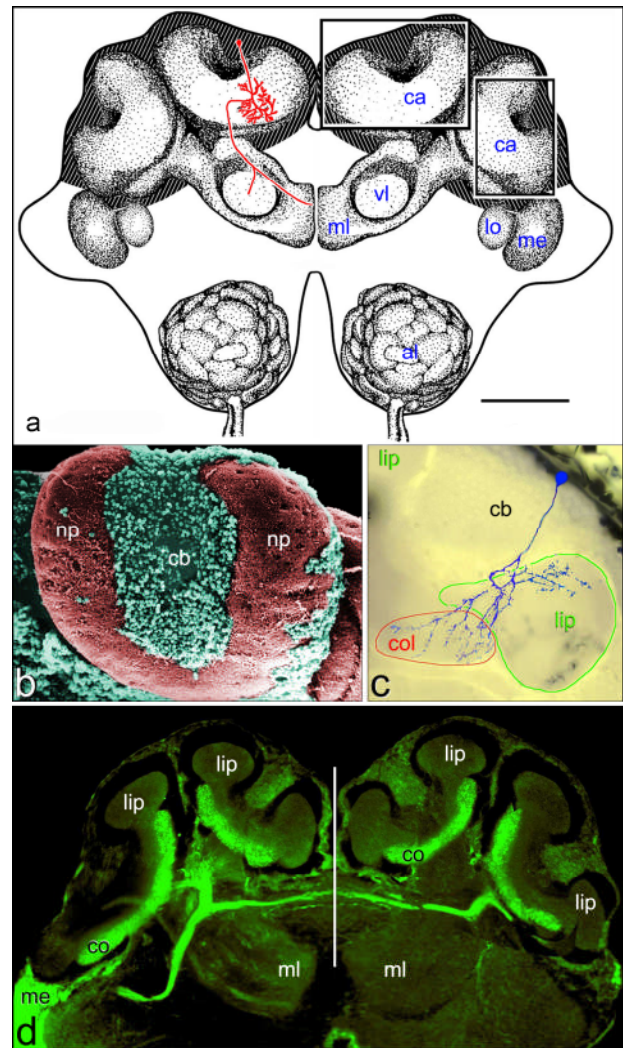


Fig. 6: (a) The mushroom bodies comprise the calyx (*ca*) and the mushroom body lobes and are composed of thousands of Kenyon cells (a single one shown in red) which receive input in the calyx. Their y-shaped axons project to both, the vertical (*vl*) and medial lobe (*ml*). (b) The calyx is composed of cup-shaped neuropils (*np*, red) around which the small cell bodies (*cb*) of the Kenyon cells are arranged (green); part of the Kenyon cell body layer is removed to reveal the neuropil. (c) The calyx is usually subdivided into a *lip* and a collar (*co*) region and most Kenyon cells receive input in one or the other region. In addition, in ants a class of Kenyon cells (blue) exists that probe both regions, *lip* and collar, with their dendrites. (d) The collar region receives visual input (green) originating from the medulla (*me*) and the lobula (*lo*) (input from lobula not shown). Approximate areas boxed in (a) are enlarged in (b) and (c), respectively; antennal lobe (*al*). Scale bar = 250  $\mu$ m.

the medulla. Output neurons from both, the medulla and the lobula project to "optic foci" in the central brain and to descending interneurons which in turn project from the brain to the thorax where they control movement (walking; flight in alates) that are guided by visual input. Part of the visual information is also sent to the mushroom bodies, central brain structures involved in learning and memory and other "advanced" neuronal processing, which will be described in the next section.

## Mushroom bodies: central control of advanced behavior

The mushroom bodies are central brain structures found in almost all insects (STRAUSFELD & al. 1998). They were first described from bees by Felix DUJARDIN (1850), who suggested them to be involved in "intelligent" control of behavior (as opposed to instincts) and their size to correlate with the degree of a species' social organization. This suggests that they should be important structures in the ant brain. The idea that mushroom bodies may be involved in learning and memory originates from lesion experiments in the brains of wood ant (*Formica*) workers and the resulting deficiency in negotiating a maze using olfactory cues (VOWLES 1964). Later, mushroom bodies have become key model systems in invertebrate learning and memory research, in particular in honeybees (ERBER & al. 1980) and in fruit flies (HEISENBERG & al. 1985). The mushroom bodies are particularly large in ant workers (Fig. 6a), their relative size (compared to the overall brain volume) being more than twice that found in honey bees (GRONENBERG & HÖLLDOBLER 1999) whereas male ants have relatively small mushroom bodies (compare Figs. 7a, b). This correlates well with the general idea that worker ants rely on behavioral plasticity (e.g., finding and remembering new food sources or adapting to changing environments) while male behavior appears more "hard-wired" or pre-programmed. The larger mushroom bodies of ant workers assumedly endow them with increased learning and memory and other cognitive abilities.

Mushroom bodies are composed of many thousands (Fig. 6b) of particularly small neurons (globuli cells or Kenyon cells; c. 130,000 in *Camponotus rufipes*, EHMER & GRONENBERG 2004). All these Kenyon cells have their dendrites in the calyx neuropil and send their axons in parallel to the vertical and medial lobes of the mushroom body (Fig. 6a). Most Kenyon cells have a y-shaped, bifurcating axon and together, these thousands of parallel axons shape the mushroom body lobes (indicated by the sketch of a Kenyon cell in Fig. 6a). Kenyon cells receive input at their dendrites in the calyx (Fig. 6a), which comprises a so-called lip and a collar region (Fig. 6c). Kenyon cells either receive olfactory input in the calyx' lip region (e.g., from olfactory neurons such as shown in Fig. 3) or visual input in the calyx' collar region (Fig. 6d, EHMER & GRONENBERG 2004). Some Kenyon cells have dendritic arborizations in both calyx regions (lip and collar, Fig. 6c) and are therefore assumed to combine visual and olfactory input information. Such "bimodal" Kenyon cells have not been found in insects other than ants (EHMER & GRONENBERG 2004).

In the calyx, visual and olfactory input neurons terminate in presynaptic structures referred to as "boutons", around which postsynaptic (receiving) elements ("spines") are arranged. Together, these miniature output/input structures form little spherical elements and give the calyx tissue a "microglomerular" texture in the light microscopic image. These microglomeruli have diameters of 1 - 5  $\mu\text{m}$  in different ant species (SEID & al. 2005, SEID & WEHNER 2007). In the calyx' visual (collar) region, the volume of individual microglomeruli and associated synapses is only about 1/3 that of microglomeruli in the olfactory (lip) region (SEID & WEHNER 2007), which the authors (SEID & WEHNER 2007) interpret as resulting in a more

reliable transmission of olfactory information compared to visual information.

The olfactory (Fig. 3) or visual input neurons (Fig. 6d) are referred to as extrinsic neurons because their cell bodies and major processes reside outside of the mushroom bodies. Extrinsic neurons provide input to the Kenyon cells or gather output from them, respectively. Besides input to the calyx, other extrinsic neurons sample the lattice of parallel Kenyon cell axons in the mushroom body lobes with their comb or brush-like dendritic trees (or axonal arborizations in the case of input neurons), receiving simultaneous input from (or sending output to) many hundreds of Kenyon cells. A hypothesis based on research in locusts and honeybees suggests that each Kenyon cell processes highly specific information, e.g., responding only to a particular stimulus combination and / or temporal coincidence, and even then only with a few action potentials ("sparse coding", PEREZ-ORIVE & al. 2002, SZYSZKA & al. 2005). Mushroom body output neurons could therefore integrate very complex spatio-temporal sensory conditions, and electrophysiology in honeybees and cockroaches revealed complex response properties that often change over time and as a consequence of previous stimuli, hence representing physiological mechanisms thought to underlie behavioral plasticity, learning and memory (MAUELSHAGEN 1993, LI & STRAUSFELD 1999). Two recent studies show complex response properties for ant mushroom body neurons comparable to those found in other insects, but only olfactory stimuli have been tested in those studies (YAMAGATA & al. 2005, 2007).

Many ants who mainly rely on chemical and tactile cues receive mainly olfactory (and probably tactile) input to their mushroom bodies while species that also rely on vision for orientation purposes have larger visual input areas in their mushroom body calyces (e.g., *Formica* wood ants, *Myrmecocustus* honey ants or *Cataglyphis* desert ants, KÜHN-BÜHLMANN & WEHNER 2006). These genera are known to use visual landmarks and other forms of visual orientation cues. This supports the idea that the mushroom bodies play a central role in memory-based orientation abilities. This idea is also supported by findings that the mushroom body size, and in particular the calyx, increases in foragers when compared to nest workers of the same size. This has first been examined in honeybees (WITHERS & al. 1993) and subsequently shown for *Camponotus floridanus* (GRONENBERG & al. 1996) and for *Cataglyphis bicolor* (KÜHN-BÜHLMANN & WEHNER 2006). While mushroom bodies are a current "hot topic" in insect neuroscience and beyond, and even though in ants the mushroom bodies are large, ants contribute little to this field as they are neither molecular nor behavioral "model systems".

### The central complex

The central complex comprises a group of unpaired structures in the central brain of arthropods: the central body (upper and lower division; also called fan-shaped body and ellipsoid body, respectively), the protocerebral bridge and the paired noduli. The central body is composed of eight or 16 subunits that are arranged in a fan-shaped fashion and interconnected by a complex arrangement of chiasmata (STRAUSFELD 1975, LOESEL & al. 2002). Some researchers suggest the central complex to be a major center for processing of polarized light information where the 16 sub-

units represent the spatial organization of polarization e-vectors (based on evidence from locusts, HOMBERG 2004, HEINZE & HOMBERG 2007). Evidence from fruit fly mutants affecting the central complex led other researchers to suggest that it is involved in limb coordination and walking control (STRAUSFELD 1999, STRAUSS 2002). The central complex communicates with other central neuropils and is (anatomically) in a position to integrate all sensory modalities and modulate ongoing motor commands sent "down" to the legs or wings. The fact that the central body comprises sets of neurons each containing different neuromodulators (LOESEL & al. 2002) suggests that it may be involved in controlling and switching entire suites of behaviors. Little is known about the central complex of ants in particular and it is likely that in ants it plays analogous roles in organizing behavior as it does in locusts or fruit flies. It looks similar to the central complex of paper wasps and general staining reveals eight major subdivisions of the upper and lower division of the central body (Figs. 7c, d), which, upon closer inspection, appear to be subdivided into two parts, as is the case in most other insects. The central body is a structure found in all ants (including blind species such as in the genus *Mystrium*), hence visual processing cannot be the sole function it serves. The central body is of similar relative size in those ant species where it has been examined. In many ant species, it appears to be relatively larger in males than it is in workers (Figs. 7c, d), just the opposite as is the case for mushroom bodies (Figs. 7a, b) or antennal lobes. As ant males in general are more "hard wired" or "pre-programmed" behaviorally, the large size of male central bodies would suggest that the central complex does not contribute to behavioral plasticity (in contrast to the mushroom bodies) but instead supports some behavioral functions that do not require learning (such as switching between behavioral contexts). Polarization vision or leg control would both fit this description.

### Brain size and plasticity in social insects

A few common rules or notions come into play when considering brain size in animals. These are generally based on vertebrates and are discussed in detail in reviews on brain evolution such as ROTH & DICKE (2005) or STRIEDTER (2005). In related taxa, brain size correlates with body size (JERISON 1973). This appears to be generally true for ants, too, and has been shown for several species of *Cataglyphis* desert ants (WEHNER & al. 2007). On average, larger ants have larger brains. However, like vertebrates, smaller insects have relatively larger brains when compared to their body or head size. This is evident when comparing a large and small worker of the same colony of leaf-cutting ants *Atta* (Figs. 8b, c). In the large soldier, the brain is just a small structure in the center of the large head capsule that is mainly filled by mandible muscle (Fig. 8b). In contrast, in the small minor worker (Fig. 8c), most of the head volume is taken up by the brain, which is smaller in absolute terms than that of the large soldier (Figs. 8e, f). This same relationship is also found across taxa where larger ants have more muscle inside their larger heads.

Brains can be miniaturized up to a certain limit, as indicated by some comparative brain volume data: large bumblebee (head width c. 4.6 mm): c. 3 mm<sup>3</sup>, honeybee (head width c. 3.6 mm): c. 1 mm<sup>3</sup> (MARES & al. 2005); carpenter ants *Camponotus* (different species; head widths c. 1.3 -

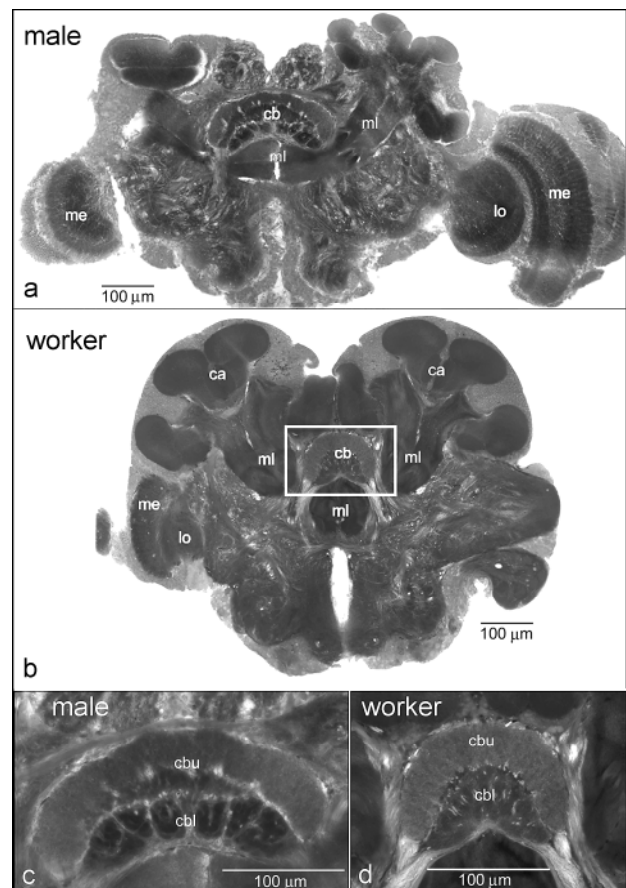


Fig. 7: Brain and central body of a male (a, c) and worker (b, d) of *Ectatomma ruidum*. Note the overall smaller brain, larger optic lobes medulla (*me*) and lobula (*lo*), and larger central body (*cb*) in males. Area boxed in (a, b) enlarged in (c, d), respectively. Mushroom body calyx (*ca*) and medial lobe (*ml*); central body's upper (*cbu*) and lower division (*cbl*).

2.4 mm): 0.15 - 0.03 mm<sup>3</sup>, seed harvester ant *Pogonomyrmex rugosus* worker (head widths c. 1.3 - 2.6 mm): c. 0.08 mm<sup>3</sup>; *Acantognathus* (head width c. 0.6 mm): 0.01 mm<sup>3</sup>, *Strumigenys* (head width c. 0.36 mm): 0.004 mm<sup>3</sup>. As we have seen (Figs. 2f, g), brain size can be reduced geometrically, but not infinitely, leading to small brains with essentially the same composition as large brains. Space is severely limited in small ants and brains probably require a minimum size in order to not lose essential behavioral capabilities or support a given behavioral repertoire.

Unlike solitary animals, in ants brain size cannot be conclusively discussed at the species level, but has to take into account the different castes and worker specialization. The most intuitive correlation is between brain size and an animal's behavioral sophistication or repertoire, because this is the purpose of any brain: to generate and control behavior. Generally, males have smaller brains (Figs. 5, 7) than females or workers, and their behavioral repertoires are reduced as males generally do not contribute much to many of the colony's tasks and in particular do not forage. Workers generally have smaller optic lobes and larger antennal lobes than males (e.g., in the ponerine ant *Harpegnathos saltator*; HOYER & al. 2005). Likewise, *Camponotus japonicus* workers have c. 430 antennal lobe glome-



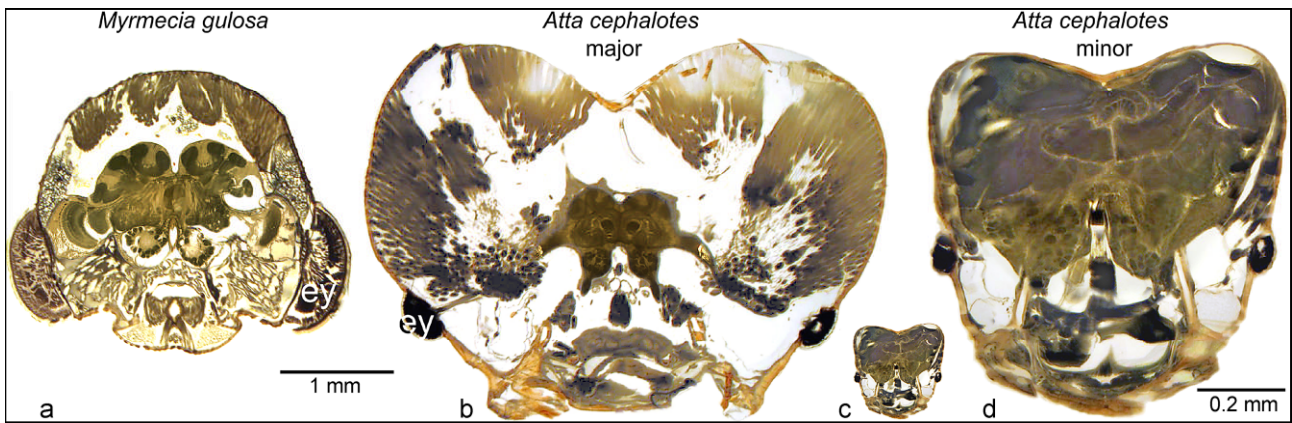


Fig. 8: Brain sizes. Frontal sections of the heads of the basal ant *Myrmecia* (a) and a major (b) and minor (c, d) of the leafcutter ant *Atta*. Head of minor *Atta* (c) enlarged in (d). Seemingly "empty" areas in the heads (a, b) are filled with hemolymph, whereas "holes" in the brain (a) represent fixation artifacts; compound eye (ey); note same scale bar for (a - c) and separate scale for (d).

ruli whereas males have only c. 215 glomeruli, NISHIKAWA & al. in press). As neural tissue is particularly expensive in metabolic terms (LAUGHLIN & al. 1998), it makes intuitively sense that ant males should have fewer glomeruli and smaller brains than workers.

What can a larger brain do that a smaller one cannot do? Small brains comprise fewer neurons, each of which will also be smaller. The volume of a "standard" ant brain can thus probably be reduced more than 100-fold, but small ants pay for the miniaturization of their nervous system (and reduced number of muscles or muscle fibers): fewer sensory structures result in reduced sensory sensitivity and ability to discriminate stimuli, fewer motor neurons result in less sophisticated movement control and behavioral repertoires and fewer and smaller interneurons should reduce the ants' cognitive abilities. Besides these general rules or assumptions, no systematic analyses exist about the effect of brain and neuron size reduction on the behavior of ants. In fact, little is known about brain miniaturization in any insects.

The sophistication that we admire in the behavior of ants is a product of the entire colony and is controlled not by a single brain, but by the sum of all the individual brains of the colony's members. In analogy to the "superorganism" (HÖLLDOBLER & WILSON 1990), this could be referred to as a "superbrain". Workers have reduced behavioral repertoires (e.g., no sexual or mating behavior and often further specialization for particular tasks) and can thus afford reduced brains compared to solitary insects. The more advanced the social system of an ant species is, the more specialized and less pluripotent are the workers (ANDERSON & MCSHEA 2001). Assuming that behavioral sophistication depends on neuronal processing power (brain size, complexity), this would imply that socially more advanced ants generally require less individual brain capacity. Hence in ants and social insects in general, sociality on average might go along with a decrease in individual brain size. This is illustrated by Fig. 8, where the evolutionarily basal bulldog ant *Myrmecia* (Fig. 8a) has a larger brain than the advanced leafcutting ant *Atta*, even though the latter (a soldier) has a larger head (Fig. 8b). The much smaller *Atta* worker (Figs. 8c, d) is less specialized and has a larger brain (relative to its head size).

However, there seems to be little published empirical evidence supporting the idea that more socially advanced ants can afford smaller brains. COLE (1985) described a positive correlation between brain size and behavioral complexity in ants, but the study is based on brain measurements by PANDAZIS (1930), which, by current morphometric standards, appear quite unreliable. This proposed relationship (more socially advanced ants may have smaller brains) is in stark contrast to that found in vertebrates (e.g., primates), where social advance goes along with considerable increase in brain size (e.g., chimpanzee brain weight c. 400 g, *Homo sapiens* c. 1400 g). The "social brain hypothesis" suggests that social vertebrates need much of their brain power to "read" and understand not only other group members' signals, but also their intentions (e.g., DUNBAR 2003). In contrast, ants (and other social insects) use mainly chemical cues for communication and do not rely on the sophisticated social cognition abilities of social vertebrates.

In a recent study, WEHNER & al. (2007) suggest that in desert ants (genus *Cataglyphis*), a species' worker brain size correlates with colony size: species with only a few hundred workers have smaller brains (compared to their body size) than species with thousands of workers, suggesting that social tasks and communication (assumed to be more demanding in larger colonies) do require some additional brain matter after all. Here then is a parallel to the rule found in primates and other social vertebrates. However, *Cataglyphis* ants are socially not particularly advanced and show little worker task specialization (other than an age-related switch from nest duties to foraging). At a grander scale, the degree of division of labor is a key indication for an ant species' social organization (ANDERSON & MCSHEA 2001), and it might go along with relative brain size reduction rather than increase.

Interestingly, in the same study, Wehner and coworkers have tried to apply to ants the brain size - body size correlation found in vertebrates (WEHNER & al. 2007). The two regression lines do not connect – ants appear to have smaller brains than (nonexistent) vertebrates of comparable body size would be expected to have. While the authors of this inspiring study discuss various causes, the main reason for the mismatch may just be what was proposed above

– that ants are social and the more socially advanced they are, the smaller their brains might be. Perhaps one should repeat the study (WEHNER & al. 2007) using flies, beetles or locusts and one might conceivably find that the general trend found for vertebrates holds for (solitary) insects, too.

The reason for the proposed reduction of brain size in evolutionary terms is that nervous tissue is metabolically particularly expensive to maintain (LAUGHLIN & al. 1998); hence, particular brain parts or neurons will be lost during evolution if they are no longer required. The same is true for an individual's life time, where neurons expand or are pruned and brains or brain components can shrink in volume. This has been most prominently shown in male song birds, where brain structures involved in song control shrink after the mating (singing) season and may expand in advance of the next mating season (NOTTEBOHM 1981). Similar brain plasticity has been shown in honeybees (WITHERS & al. 1993) and in ants (GRONENBERG & al. 1996, KÜHN-BÜHLMANN & WEHNER 2006), in which the mushroom bodies increase in size during the workers' transition from working inside the nest to becoming outside foragers, a task that is more demanding with respect to cognitive abilities. Besides experience, mushroom bodies also change in size in an age-dependent or "experience expectant" manner (FAHRBACH & al. 1998). Complex experiences, such as are associated with foraging activity, probably give rise to the modification, growth and addition of many synapses (points of information transfer between nerve cells), which in turn presumably result in the observed changes of brain volume.

In contrast to this size increase, the entire brain, and the optic lobes in particular, shrink in female ants once they are mated (JULIAN & GRONENBERG 2002) or in substitute queens (gamergates, GRONENBERG & LIEBIG 1999): virgin females need a full behavioral repertoire during their mating flights, but once they shed their wings and start living underground, the queens do not rely on vision any more and can discard part of their "expensive" brain. Hence ants have large brains only when they need it and brain size adapts to the changing behavioral requirements during an ant's life time. This brain plasticity may be more common across insects than originally thought, but it has mainly been studied in social insects.

### Conclusion

We have seen that, like in other insects, ant brains are composed of sensory, motor and multimodal central components. What is special about ant brains is not an individual brain component, but the overall composition of the brains with a major emphasis on olfactory and pheromone processing and relatively less prominence of visual processing. Another hallmark of ant brain composition is the large size of their mushroom bodies. Many ant foragers may be specialized for finding and remembering new food sources and efficient spatial navigation back to the nest, functions which assumedly are supported by the mushroom bodies. In this context, it would be interesting to compare mushroom bodies in scouts and foragers that rely on memory vs. ones that "simply" follow pheromone trails.

Unlike in vertebrates, there are no specific "social" brain components (except the increased capacity for processing pheromone information). The social life style and division of labor may have lead to potential brain reduction rather than increase: specialized workers do not need the

brain substrate required for sexual behaviors and other general tasks. It is the interaction and communication of many small brains – through their vehicles, the individual ant workers – from which emerges the complex behavior of an ant colony, without a single master brain being in control. Brain size is further dynamically controlled by the individual's need for neuronal processing power during its life time, hence no metabolic energy is wasted on unnecessary neural tissue. Ant brains thus appear well adapted at the individual and colony level. The social life style of ants is based on inter-individual communication, and future research should try to establish how ant brains allow the complex communication signals to be generated and analyzed. Little is known about pheromone processing in ant brains, and next to nothing about the generation, perception and analysis of touch and vibratory communication signals by the brain.

### Zusammenfassung

Dieser Artikel fasst den aktuellen Kenntnisstand zum Gehirn der Ameisen im Kontext mit ihrem Verhalten zusammen. Arbeitsteilung ist die Basis der sozialen Lebensweise von Ameisen; sie resultiert nicht nur in einer Spezialisierung des Verhaltens, sondern auch in einigen Anpassungen der Ameisengehirne. Ich beschreibe hier die Struktur und Funktion der wichtigsten Neuropile (visuelle und olfaktorische Zentren sowie zentrale multi-sensorische integrative Kompartimente des Gehirns) zusammen mit einigen ihrer Neuronen. Im Gegensatz zu sozialen Wirbeltieren, die größere Gehirne als solitäre Arten haben, sind die Gehirne von Ameisen nicht größer als jene solitärer Insekten; sie sind aber stärker spezialisiert. Der biologische Erfolg von Ameisen ist wahrscheinlich weniger das Resultat der Gehirne von Einzelindividuen als das Resultat des Zusammenspiels hunderter oder tausender Gehirne einer Kolonie.

### References

- ANDERSON, C. & MCSHEA, D.W. 2001: Individual versus social complexity, with particular reference to ant colonies. – *Biological Reviews* 76: 211-237.
- BORST, A. & HAAG, J. 2002: Neural networks in the cockpit of the fly. – *Journal of Comparative Physiology A* 188: 419-437.
- BRISCOE, A.D. & CHITTKA, L. 2001: The evolution of color vision in insects. – *Annual Review of Entomology* 46: 471-510.
- BURLING-THOMPSON, C. 1913: A comparative study of the brains of three genera of ants, with special reference to the mushroom bodies. – *Journal of Comparative Neurology* 23: 515-572.
- CHAMBILLE, I., MASSON, C. & ROSPARS, J.P. 1980: The deutocerebrum of the cockroach *Blaberus craniifer* BURM.: Spatial organization of the sensory glomeruli. – *Journal of Neurobiology* 11: 135-157.
- COLE, B.J. 1985: Size and behavior in ants: Constraints and complexity. – *Proceedings of the National Academy of Sciences of the United States of America* 82: 8548-8551.
- DUJARDIN, F. 1850: Mémoire sur le système nerveux des insectes. – *Annales des Sciences Naturelles* 14: 195-205.
- DUMPERT, K. 1972: Alarmstoffrezeptoren auf der Antenne von *Lasius fuliginosus* (LATR.) (Hymenoptera Formicidae). – *Zeitschrift für Vergleichende Physiologie* 76: 403-425.
- DUNBAR, R.I.M. 2003: The social brain: mind, language, and society in evolutionary perspective. – *Annual Review of Anthropology* 32: 163-81.

- DUPUY, F., SANDOZ, J.-C., GIURFA, M. & JOSENS, R. 2006: Individual olfactory learning in *Camponotus* ants. – *Animal Behaviour* 72: 1081-1091.
- EHMER, B. & GRONENBERG, W. 1997: Proprioceptors and fast antennal reflexes in the ant *Odontomachus* (Formicidae, Ponerinae). – *Cell and Tissue Research* 290: 153-165.
- EHMER, B. & GRONENBERG, W. 2004: Mushroom body volumes and visual interneurons in ants: comparison between sexes and castes. – *Journal of Comparative Neurology* 469: 198-213.
- ERBER, J., MASUHR, T. & MENZEL, R. 1980: Localization of short-term memory in the brain of the bee, *Apis mellifera*. – *Physiological Entomology* 5: 343-358.
- FAHRBACH, S.E., MOORE, D., CAPALDI, E.A., FARRIS, S.M. & ROBINSON, G.E. 1998: Experience-expectant plasticity in the mushroom bodies of the honeybee. – *Learning and Memory* 5: 115-123.
- FLANAGAN, D. & MERCER, A.R. 1989: An atlas and 3-D reconstruction of the antennal lobes in the worker honey bee, *Apis mellifera* L. (Hymenoptera: Apidae). – *International Journal of Insect Morphology and Embryology* 18: 145-159.
- GALIZIA, C.G., MENZEL, R. & HÖLLDOBLER, B. 1999: Optical imaging of odor-evoked glomerular activity patterns in the antennal lobes of the ant *Camponotus rufipes*. – *Naturwissenschaften* 86: 533-537.
- GOLL, W. 1967: Strukturuntersuchungen am Gehirn von *Formica*. – *Zeitschrift für Morphologie und Ökologie der Tiere* 59: 143-210.
- GREINER, B., NARENDRA, A., REID, S.F., DACKE, M., RIBI, W.A. & ZEIL, J. 2007: Eye structure correlates with distinct foraging-out timing in primitive ants. – *Current Biology* 17: 879-880.
- GRONENBERG, W., HEEREN, S. & HÖLLDOBLER, B. 1996: Age-dependent and task-related morphological changes in the brain and the mushroom bodies of the ant *Camponotus floridanus*. – *Journal of Experimental Biology* 199: 2011-2019.
- GRONENBERG, W. & HÖLLDOBLER, B. 1999: Morphologic representation of visual and antennal information in the ant brain. – *Journal of Comparative Neurology* 412: 229-240.
- GRONENBERG, W. & LIEBIG, J. 1999: Smaller brains and optic lobes in reproductive workers of the ant *Harpegnathos*. – *Naturwissenschaften* 86: 343-345.
- HANSSON, B.S. 2002: A bug's smell – research into insect olfaction. – *Trends in Neuroscience* 25: 270-274.
- HEINZE, S. & HOMBERG, U. 2007: Maplike representation of celestial e-vector orientations in the brain of an insect. – *Science* 315: 995-997.
- HEISENBERG, M., BORST, A., WAGNER, S. & BYERS, D. 1985: *Drosophila* mushroom body mutants are deficient in olfactory learning. – *Journal of Neurogenetics* 2: 1-30.
- HILDEBRAND, J.G. & SHEPHERD, G.M. 1997: Mechanism of olfactory discrimination: converging evidence for common principles across phyla. – *Annual Review of Neuroscience* 20: 595-631.
- HÖLLDOBLER, B. & WILSON, E.O. 1990: The ants. – Belknap Press of Harvard University Press, Cambridge, MA, 732 pp.
- HOMBERG, U. 2004: In search of the sky compass in the insect brain. – *Naturwissenschaften* 91: 199-208.
- HOYER, S.C., LIEBIG, J. & RÖSSLER, W. 2005: Biogenic amines in the ponerine ant *Harpegnathos saltator*: serotonin and dopamine immunoreactivity in the brain. – *Arthropod Structure & Development* 34: 429-440.
- JERISON, H.J. 1973: Evolution of the brain and intelligence. – Academic Press, New York, 267 pp.
- JULIAN, G.E. & GRONENBERG, W. 2002: Smaller brains in queen ants. – *Brain, Behavior and Evolution* 60: 152-164.
- JUST, S. & GRONENBERG, W. 1999: The control of mandible movements in the ant *Odontomachus*. – *Journal of Insect Physiology* 45: 231-240.
- KENYON, F.C. 1896: The brain of the bee. – *Journal of Comparative Neurology* 6: 133-210.
- KIEPENHEUER, J. 1971: Farbunterscheidungsvermögen bei der roten Waldameise *Formica polyctena* FOERSTER. – *Zeitschrift für Vergleichende Physiologie* 75: 86-104.
- KLEINEIDAM, C.J., OBERMAYER, M., HALBICH, W. & RÖSSLER, W. 2005: A macroglomerulus in the antennal lobe of leaf-cutting ant workers and its possible functional significance. – *Chemical Senses* 30: 383-392.
- KLEINEIDAM, C., ROMANI, R., TAUTZ, J. & ISIDORO, N. 2000: Ultrastructure and physiology of the CO<sub>2</sub> sensitive sensillum ampullaceum in the leaf-cutting ant *Atta sexdens*. – *Arthropod Structure & Development* 29: 43-55.
- KLOTZ, J.H., REID, B.L. & GORDON, W.C. 1992: Variation of ommatidia number as a function of worker size in *Camponotus pennsylvanicus* (DEGEER) (Hymenoptera: Formicidae). – *Insectes Sociaux* 39: 233-236.
- KORSCHING, S.I. 2001: Odor maps in the brain: Spatial aspects of odor representation in sensory surface and olfactory bulb. – *Cellular and Molecular Life Sciences* 58: 520-530.
- KRETZ, R. 1979: A behavioral analysis of color vision on the ant *Cataglyphis bicolor* (Hymenoptera: Formicidae). – *Journal of Comparative Physiology A* 131: 217-233.
- KÜHN-BÜHLMANN, S. & WEHNER, R. 2006: Age-dependent and task-related volume changes in the mushroom bodies of visually guided desert ants, *Cataglyphis bicolor*. – *Journal of Neurobiology* 66: 511-521.
- LAUGHLIN, S.B., DE RUYTER VAN STEVENINCK, R.R. & ANDERSON, J.C. 1998: The metabolic cost of neural information. – *Natural Neuroscience* 1: 36-41.
- LI, Y. & STRAUSFELD, N.J. 1999: Multimodal efferent and recurrent neurons in the medial lobes of cockroach mushroom bodies. – *Journal of Comparative Neurology* 409: 647-663.
- LIEKE, E. 1981: Graded and discrete receptor potentials in the compound eye of the Australian bulldog-ant (*Myrmecia gulosa*). – *Biological Cybernetics* 40: 151-56.
- LOESEL, R., NÄSSEL, D.R. & STRAUSFELD, N.J. 2002: Common design in a unique midline neuropil in the brains of arthropods. – *Arthropod Structure & Development* 31: 77-91.
- LOPEZ-RIQUELME, G.O., MALO, E., CRUZ-LOPEZ, L. & FANJUL-MOLES, M.L. 2006: Antennal olfactory sensitivity in response to task-related odours of three castes of the ant *Atta mexicana* (Hymenoptera: Formicidae). – *Physiological Entomology* 31: 353-360.
- LUBBOCK, SIR J. 1881: Observations on ants, bees, and wasps. IX. Color of flowers as an attraction to bees: Experiments and considerations thereon. – *Journal of the Linnean Society London (Zoology)* 16: 110-112.
- MARES, S., ASH, L. & GRONENBERG, W. 2005: Brain allometry in bumblebee and honey bee workers. – *Brain, Behavior and Evolution* 66: 50-61.
- MARTINOYA, C., BLOCH, S., VENTURA, D. & PUGLIA, N.M. 1975: Spectral efficiency as measured by ERG in the ant (*Atta sexdens rubrospinosa*). – *Journal of Comparative Physiology* 104: 205-210.
- MAUELSHAGEN, J. 1993: Neural correlates of olfactory learning paradigms in an identified neuron in the honeybee brain. – *Journal of Neurophysiology* 69: 609-625.
- MCLEMAN, M.A., PRATT, S.C. & FRANKS, N.R. 2002: Navigation using visual landmarks by the ant *Leptothorax albipennis*. – *Insectes Sociaux* 49: 203-208.

- MENZEL, R. & KNAUT, R. 1973: Pigment movement during light and chromatic adaptation in the retinula cells of *Formica polyctena* (Hymenoptera, Formicidae). – *Journal of Comparative Physiology* 86: 125-38.
- MENZEL, R. & WEHNER, R. 1970: Augenstrukturen bei verschiedenen grossen Arbeiterinnen von *Cataglyphis bicolor* FABR. (Formicidae, Hymenoptera). – *Zeitschrift für Vergleichende Physiologie* 68: 446-449.
- MOTE, M.I. & WEHNER, R. 1980: Functional characteristics of photoreceptors in the compound eye and ocellus of the desert ant, *Cataglyphis bicolor*. – *Journal of Comparative Physiology* 137: 63-71.
- NISHIKAWA, M., NISHINO, H., MISAKA, Y., KUBOTA, M., TSUJI, E., SATOJI, Y., OZAKI, M. & YOKOHARI, F. in press: Sexual Dimorphism in the Antennal Lobe Structure of the Ant, *Camponotus japonicus*. – *Zoological Science (Japan)*.
- NOTTEBOHM, F. 1981: A brain for all seasons: cyclical anatomical changes in song control nuclei of the canary brain. – *Science* 214: 1368-1370.
- PANDAZIS, G. 1930: Über die relative Ausbildung der Gehirnzentren bei biologisch verschiedenen Ameisenarten. – *Zeitschrift für Morphologie und Ökologie der Tiere* 18: 114-169.
- PEREZ-ORIVE, J., MAZOR, O., TURNER, G.C., CASSENAER, S., WILSON, R.I. & LAURENT, G. 2002: Oscillations and sparsening of odor representations in the mushroom body. – *Science* 297: 359-365.
- RAMON, F. & GRONENBERG, W. 2005: Electrical potentials indicate stimulus expectancy in the brains of ants and bees. – *Cellular and Molecular Neurobiology* 25: 313-327.
- ROCES, F. 1994: Odour learning and decision-making during food collection in the leaf-cutting ant *Acromyrmex lundii*. – *Insectes Sociaux* 41: 235-239.
- ROSPARS, J.P. & HILDEBRAND, J.G. 2000: Sexually dimorphic and isomorphic glomeruli in the antennal lobe of the Sphinx moth *Manduca sexta*. – *Chemical Senses* 25: 119-129.
- ROTH, G. & DICKE, U. 2005: Evolution of the brain and intelligence. – *Trends in Cognitive Sciences* 9: 250-257.
- SEID, M.A., HARRIS, K.M. & TRANIELLO, J.F.A. 2005: Age-related changes in the number and structure of synapses in the lip region of the mushroom bodies in the ant *Pheidole dentata*. – *Journal of Comparative Neurology* 488: 269-277.
- SEID, M.A. & WEHNER, R. 2007: Ultrastructure and synaptic differences of the boutons of the projection neurons between the lip and collar regions of the mushroom bodies in the ant, *Cataglyphis albicans*. – *Journal of Comparative Neurology* 507: 1102-1108.
- STOCKER, R.F. 1994: The organization of the chemosensory system in *Drosophila melanogaster*: a review. – *Cell and Tissue Research* 275: 3-26.
- STRAUSFELD, N.J. 1976: Atlas of an insect brain. – Springer, Heidelberg, 145 pp.
- STRAUSFELD, N.J. 1989: Beneath the compound eye: neuroanatomical analysis and physiological correlates in the study of insect vision. In: STAVENGA, D.G. & HARDIE, R.C. (Eds.): Facets of vision. – Springer, Heidelberg, New York, pp. 318-359.
- STRAUSFELD, N.J. 1999: A brain region in insects that supervises walking. – *Progress in Brain Research* 123: 273-284.
- STRAUSFELD, N.J., HANSEN, L., LI, Y., GOMEZ, R.S. & ITO, K. 1998: Evolution, discovery, and interpretation of arthropod mushroom bodies. – *Learning and Memory* 5: 11-37.
- STRAUSS, R. 2002: The central complex and the genetic dissection of locomotor behaviour. – *Current Opinion in Neurobiology* 12: 633-638.
- STRIEDTER, G.F. 2005: Principles of brain evolution. – Sinauer, Sunderland, MA, 280 pp.
- SZYSZKA, P., DITZEN, M., GALKIN, A., GALIZIA, C.G. & MENZEL, R. 2005: Sparsening and temporal sharpening of olfactory representations in the honeybee mushroom bodies. – *Journal of Neurophysiology* 94: 3303-3313.
- VOSSHALL, L.B., WONG, A.M. & AXEL, R. 2000: An olfactory sensory map in the fly brain. – *Cell* 102: 147-159.
- VOWLES, D.M. 1964: Olfactory learning and brain lesions in the wood ant (*Formica rufa*). – *Journal of Comparative Physiology and Psychology* 58: 105-111.
- WEHNER, R. 1994: The polarization-vision project: championing organismic biology. – *Fortschritte der Zoologie* 59: 103-143.
- WEHNER, R. 2003: Desert ant navigation: How miniature brains solve complex tasks. – *Journal of Comparative Physiology A* 189: 579-588.
- WEHNER, R., FUKUSHI, T. & ISLER, K. 2007: On being small: Brain allometry in ants. – *Brain, Behavior and Evolution* 69: 220-228.
- WEHNER, R. & MENZEL, R. 1969: Homing in the ant *Cataglyphis bicolor*. – *Science* 164: 192-194.
- WITHERS, G.S., FAHRBACH, S.E. & ROBINSON, G.E. 1993: Selective neuroanatomical plasticity and division of labour in the honeybee. – *Nature* 364: 238-240.
- YAMAGATA, N., FUJIWARA-TSUIJI, N., YAMAOKA, R. & MIZUNAMI, M. 2005: Pheromone communication and the mushroom body of the ant, *Camponotus obscuripes* (Hymenoptera: Formicidae). – *Naturwissenschaften* 92: 532-536.
- YAMAGATA, N., NISHINO, H. & MIZUNAMI, M. 2006: Pheromone-sensitive glomeruli in the primary olfactory centre of ants. – *Proceedings of the Royal Society B* 273: 2219-2225.
- YAMAGATA, N., NISHINO, H. & MIZUNAMI, M. 2007: Neural pathways for the processing of alarm pheromone in the ant brain. – *Journal of Comparative Neurology* 505: 424-442.
- ZUBE, C., KLEINEIDAM, C.J., KIRSCHNER, S., NEEF, J. & RÖSSLER, W. 2008: Organization of the olfactory pathway and odor processing in the antennal lobe of the ant *Camponotus floridanus*. – *Journal of Comparative Neurology* 506: 425-441.