

Review article

Associative learning in honey bees

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Summary — The learning behavior of honey bees has been reviewed. In the context of foraging behavior, bees perform 2 forms of learning, latent (or observatory) and associative learning. Latent learning plays an important role in spatial orientation and learning during dance communication, but the mechanisms of this kind of learning are little understood. In associative learning, stimuli experienced immediately before the reward (usually sucrose solution) are memorized for the guidance of future behavior. Well-established paradigms have been used to characterize operant and classical conditioning. The classical conditioning of olfactory stimuli is a very effective form of learning in bees and has helped to describe the behavioral and physiological basis of memory formation. It is concluded that memory needs time to be established and is processed in sequential phases. The neuronal compartments of the brain involved in the chemosensory pathway appear to participate differently in the sequential memory phases. A model is developed which assigns the strong non-associative components in olfactory conditioning to the antennal lobes, and the associative components to the mushroom bodies and the lateral output region of the protocerebrum. It is speculated that the amnesia-sensitive memory resides in the mushroom bodies and the amnesia-resistant memory in certain structures (eg the lateral protocerebrum) perhaps together with the mushroom bodies.

learning / olfactory conditioning / memory / protocerebrum / mushroom bodies / *Apis mellifera*

INTRODUCTION

The social life of the honey bee (*Apis mellifera* L) colony forms the evolutionary framework for the behavior of the individual insect and is crucial for the survival of each bee, as it cannot exist independently. The lifespan of the individual bee is relatively short (4–6 wk in summer, several months in autumn, winter and spring), but the colony itself is potentially everlasting.

Bees foraging for food (nectar and pollen for the colony storehouse), water and resin (for colony care purposes) commence their foraging trips at the colony and return to it within minutes or hours. As young bees, they learn the landmarks surrounding the nest location on self-training flights. They also learn to orientate themselves to the sun compass in relation to the landmarks surrounding the nest. When the colony reproduces, a large number of

the well-experienced bees leave the colony, together with the old queen, in search of a new nesting place. During this process, each bee has to replace the old memory of its terrestrial and celestial orientation cues with a new memory (Lindauer, 1955, 1959, 1967; von Frisch, 1967). Food is collected from flowers when and wherever available and is stored for periods of starvation. Consequently, the innate search image for food sources has to be very general, and individual associative learning processes are most important for the effective accomplishment of foraging activities. Celestial and terrestrial cues, position in relation to landmarks and features (color, shape, odor, etc) of the new feeding place are learned afresh for each new location. An individual bee may collect food from only one location and one kind of flower during its lifetime, but in most cases, each bee will visit many different places and learn many different flower cues throughout its lifespan.

Within the colony, the foragers communicate using ritualized body movements (waggle dance), which encode the distance, direction and relative profitability of the food source. The odor of the food source can be smelled by the attending bees from the hairy body of the dancing bee and, in the case of nectar collection, the collected food may be sampled, as the dancer offers minute amounts for tasting. The relative profitability of the food source is estimated by the foraging bee on the basis of how quickly its sample is taken up by the young receiving bees at the colony entrance. Since the young receiving bees register the needs of the colony (brood condition, storage space, size and density of the colony) and the quality of the incoming food, the feedback to the individual forager provides the necessary information for quick adjustments to the colony's needs and a relative rating of its foraging behavior (von Frisch, 1967; Seeley, 1985a, b).

The study of learning in bees has focused on appetitive learning in the context of food collection, because experimentation is most convenient under these conditions: stimuli are easily selected and stimulus-response conditions can be accurately controlled. Since an average colony contains > 40 000 foraging bees, a virtually unlimited number of test animals are available and can be motivated to search for food by means of the recruitment behavior of experienced bees. Motivation for both recruitment and search behavior can be manipulated by the concentration of the sucrose reward. Because bees learn very fast (often by a single trial), experimentation is facilitated. The experimental insect returns to the artificial feeding station reliably and shuttles back and forth between the colony and the feeding station at intervals of minutes. Choice behavior can be easily tested because extinction procedures have little effect and search motivation is high. The training procedure of individually marked bees is also used effectively to study other forms of learning (eg latent learning during orientation to celestial and terrestrial cues) and cooperative behavior in the colony (dance communication, allocation of social duties) (von Frisch, 1967; Lindauer, 1967; Menzel, 1985; Seeley, 1985b; Gould, 1986b).

Genetic predispositions to learning may be of particular importance in insects. It is often assumed, though with limited experimental verification, that the small brain of an insect (in the bee: 1 mm³, 900 000 neurons) might be more effective if it had a particularly large proportion of stereotyped behaviors, genetically controlled connections and a preprogrammed switchboard of potential neural contacts. In other words, sensory cues may be preordained, motor programs adjusted only within strict limits, reinforcing conditions preprogrammed so that associations can be formed quickly but selectively, and internal memory pro-

cesses may run under the tight control of automatic storage routines (Gould and Marler, 1984; Menzel, 1984). In view of this, it is astounding how adaptable the behavior of bees actually is, how important learning phenomena are, how persistent the memories are, and how many signals and motor programs are learned. The genetic frame for learning has, therefore, to be quite broad in order to allow the establishment of new neural connections under the conditions of learning rules (Menzel, 1990; Menzel *et al.*, 1993).

APPETITIVE LEARNING IN THE NATURAL CONTEXT

When a searching bee discovers a source of sweet solution, *eg* an artificial feeder with sucrose solution, it quickly learns to associate the surrounding visual and olfactory signals with the reward. Acquisition functions indicate that olfactory stimuli (*eg* floral odorants) are learned within 1–2 learning trials, colors within 1–5 learning trials, and black and white patterns from the 5th learning trial onward. Most of this learning is forward conditioning, because signals perceived before the reward are most strongly associated, whereas those perceived during the reward or during the departure flight are associated less effectively or not at all.

More recently, it has been demonstrated that bees perform a specific behavior on departure, which leads to learning of new and unexpected cues (Lehrer, 1991). If visual cues are different from those experienced before, the bee does not fly away immediately after completion of feeding, but rather turns around in flight and looks back at the feeding place. The occurrence of this behavior correlates with the choice behavior at the next visit. It is therefore concluded that bees learn the new conditions during their look-back behavior.

However, it is not known whether this behavior indicates a backward conditioning, because the unconditioned stimulus has not yet been identified for this kind of learning.

During departure from a newly-discovered natural food source, the bees perform circular flights at an increasing distance from the feeding place. Most learning during this phase is directed towards more distant signals such as landmarks, celestial cues and the direction of and distance between the food source and the colony. It is not known what kind of learning guides the bee during the circular observatory flights. Associative learning is unlikely, because bees transported to an unknown place perform the same circling flights and learn to fly back to the hive along the shortest possible route without being fed at the release site (Menzel, 1989). What bees report through their dance behavior within the colony also relates to their experience during the return flight to the colony. It appears from these results that both forward and observatory learning are effective in learning of freely-flying bees.

Long-distance orientation (usually up to several kilometers) requires the learning of signal sequences and the retrieval of context-specific memories. It is indeed possible to train bees to different visual cues in a sequence within one foraging bout (Collett and Kelber, 1988). They also learn to associate a particular time of day with a particular set of stimuli (*eg* flight direction, distance, color or odor) (von Frisch, 1967).

Reversal learning, overlearning and multireversal learning are effective learning phenomena. The speed of reversal learning in a dual forced-choice situation is at first retarded in proportion to the increasing number of initial learning trials on 1 of 2 alternatives, and strongest resistance to reversal learning is reached after 5–10 initial trials. If the number of initial learning trials exceeds 10 trials, reversal to the other al-

ternative is increasingly favored (overlearning reversal effect) (Menzel, 1969). Such an overlearning reversal effect is also known to exist in other animals and is interpreted either as a loss of US strength of expected (already learned) signals or a loss of attention to the conditioned stimuli (CS) as a result of a general decrease in motivation (Rescorla and Wagner, 1972). In bees, the general motivation does not change throughout the series of learning trials, which might indicate a decrease in the associative strength in predicted US presentations as a mechanism. Multireversal schedules with fixed performance schedules reveal a learning strategy that, after many reversals, leads to a decrease in the number of reversed learning trials necessary to reach a constant level of choice preference. This would seem to indicate an acquired strategy to assimilate reversal learning (Meineke, 1978; Bitterman, 1988). However, the effect is quite small and depends greatly on the design of the experiment and the conditioned stimuli used (Menzel, 1990).

The experimental procedures which test the ability of an insect to adapt its performance to reward schedules are Skinner's (1938) continuous, fixed ratio and fixed interval reinforcement schedules (CR, FR and FI respectively). Bees develop a higher resistance to extinction in a FR than in a CR schedule. In an FI reinforcement schedule, bees show lower response rates than those in an FR schedule. FR schedules of up to 1 reinforcement out of 30 trials and FI schedules with up to 90 s between reinforcements are reached after several days of training (Grossmann, 1973). This behavior appears to be an adaptation to ecological conditions, since only a fraction of the flowers on which bees alight provide nectar and/or pollen, and these rewards are usually minute. Additional operant learning phenomena in honey bees were studied in the tradition of

experimental psychology and have been reported by Bitterman (1988).

The study of operant and latent learning in bees in a natural behavioral context has provided many examples of impressive and complex actions (von Frisch, 1967). How complex is the mind of the honey bee? Are there indications of mental operations that, in the absence of behavioral acts, may be interpreted as internal operations of learned representations? When a bee is transported in a dark box from the hive to any site within its foraging area (≈ 2 km radius), it will recognize the landmarks surrounding the hive very well and return to it reliably and quickly. Do bees under these conditions consult a mental map of the landmarks which would allow them to calculate the shortest flight path, although they have never experienced this flight path before?

Gould (1986a) reported experiments which appear to favor such an interpretation. Recent experiments, however, support the conclusion that bees use a different strategy (Wehner and Menzel, 1990). They appear to apply a hierarchy of best-matching rules to different kinds of orientation marks. The celestial cues (sun, polarized light pattern) rank highest. Bees always start to fly according to the sun compass. If that flight path produces a mismatch with the long distance landmarks (landmarks without motion parallax, *eg* profile of horizon) they gradually switch to these landmarks and fly according to the best match between the memorized and the actually experienced pattern. When this flight path brings them close to local landmarks (landmarks with motion parallax) in the hive surroundings (or the feeding place if they are motivated for foraging), then they home in by a successive search for the best match with the local landmarks (Cartwright and Collett, 1983). The rank order of the orientation marks (celestial, distant and local cues) and the

precision with which the matching is applied depends on the level of experience regarding each of these orientation marks. It thus appears that mental operations on a representational level have not to be assumed to explain the impressive capability of bees during long-distance flights.

REFLEX CONDITIONING

Classical conditioning of reflexes is a most convenient way to study the behavioral and neural mechanisms of associative learning. In the honey bee, proboscis extension reflex (PER) to a sucrose stimulus at the antennae is a reliable reflex in the context of feeding. The bee will extend its proboscis (tongue) reflexively when the antennae are touched with a drop of sucrose solution. It can be conditioned to olfactory or mechanical stimuli (conditioned stimuli, CS), even under conditions where the insect is harnessed in a tube (Kuwabara, 1957) or prepared for physiological studies (Menzel *et al*, 1974, 1991, 1993; Menzel, 1990). The PER and its conditioning to a CS is highly dependent on hunger-induced motivation.

The associative nature of PER conditioning has been established by demonstrating that only forward pairing of CS–US sequences are effective in various control groups (unpaired CS and US, CS or US only presentations), and *via* differential conditioning of the 2 olfactory stimuli. The predictive value of the CS depends on the reliability with which it is causally related to the US. For example, repeated exposure to the CS in unpaired trials reduces its acquisition in subsequent conditioning. In differential conditioning, the reversal to the initially unpaired stimulus is slower after more frequent initial unreinforced pre-exposure than after a lesser number of pre-exposures. The same applies for US-only pre-exposures in an otherwise rein-

forced context. Partial reinforcement schedules have little effect on the acquisition function, because extinction trials do not alter the CR probability but increase the resistance to extinction and other measures of learning (Menzel, 1990).

Blocking and overshadowing experiments are used to characterize the informational content of the CS (Rescorla, 1988). In PER conditioning, olfactory stimuli overshadow mechanical stimuli, and blocking effects are not found. This indicates that attentiveness is not a limiting factor, and that the salience or associability of a stimulus (olfactory over mechanical) is an important factor. Second-order conditioning is a procedure which tests whether a CS can acquire the potential of an US. This has also been demonstrated for olfactory PER conditioning (Bitterman *et al*, 1983; Menzel, 1990). The strength of the effect is highly dependent on the CS used. Citral, a particularly salient CS and chemical component of an attraction pheromone produced by bees to mark food sources, has the strong potential of an acquired US; more neutral odors (*eg* octanal) have a weak potential for second-order conditioning.

SEQUENTIAL MEMORY PROCESSING

A stable lifelong memory is formed even after only a few learning trials. Harnessed bees prepared for olfactory PER conditioning do not survive long enough to allow testing of their memory over periods of > 2–3 d, but retention remains high during this period, even after only 1–3 conditioning trials. After a single learning trial, the retention curve follows an early biphasic time course and a slowly decreasing slope in the long-term range (fig 1). The early memory phase in the minute range is particularly susceptible to both extinction and reversal learning, whereas the consolidat-

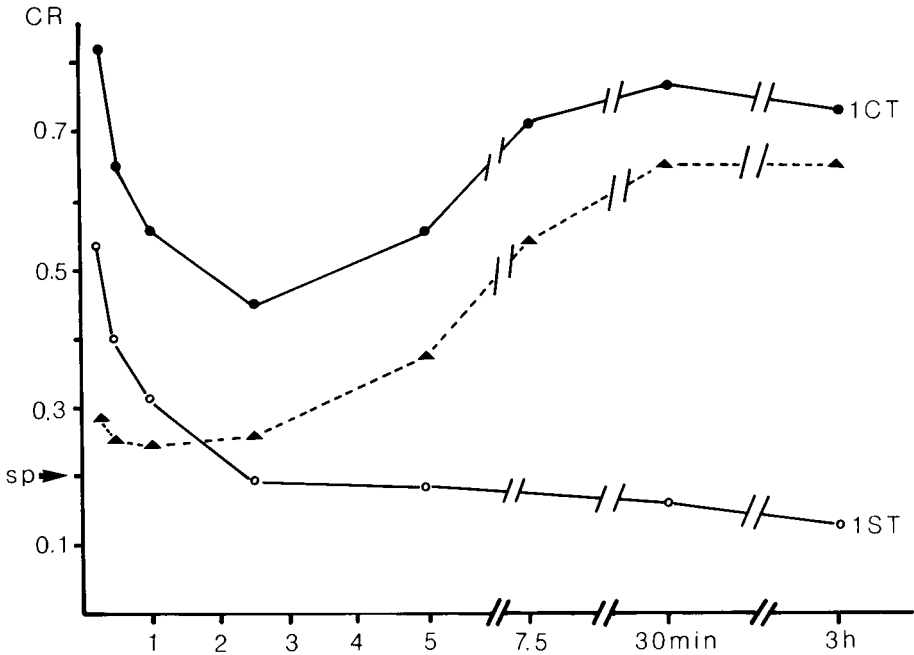


Fig 1. Time course of the response probability (CR, ordinate) to the CS (carnation odor) in 1 PER conditioning trial (curve: 1 CT) or 1 PER sensitization trial (curve: 1 ST). In the case of conditioning, each bee was conditioned by a forward pairing of CS and US at time zero. The bee was tested once at one of the indicated time intervals (abscissa) by presenting the CS alone. The curve gives the results for 921 animals. Similarly, in the case of a 1-trial sensitization, each bee was stimulated with sucrose at the antennae and the proboscis for 2 s, and then tested for its response to carnation odor once at any of the intervals indicated on the abscissa (2 057 insects tested). Sp on the ordinate indicates the spontaneous response level of all test animals 10 min before the conditioning or sensitization trial. The dotted curve indicates the associative component and is derived by subtracting the 1 ST curve from the 1 CT curve.

ed memory is much more resistant. The sensitizing effect of the appetitive stimulus (sucrose solution) overlaps with the early high response level, indicating that, at least in PER conditioning, the nonassociative memory initiated by the US contributes substantially to the response probability immediately after the single learning trial (fig 1). The specific associative memory increases slowly over 5–7 min; thus consolidation is a purely associative pro-

cess (Menzel *et al*, 1991). Genetic lines of bees with poor learning performance lack the typical biphasic retention function, and are poor in both the early nonassociative component and the associative consolidation (Brandes *et al*, 1988; Brandes and Menzel, 1990).

Amnesic treatments (cooling, narcosis, weak electroconvulsive brain stimulation (EBS)) erase the memory trace if applied within minutes of the single-trial learning.

Several trials within a minute or longer time intervals after a single trial render the memory trace immune to amnestic treatment. The time course of retrograde amnestic sensitivity is independent of the kind of learning (operant color learning, olfactory PER-conditioning), but depends on the structure of the brain to which the treatment is applied. Local cooling of the peripheral olfactory neuropile (antennal lobes) within 1 min after the learning trial causes retrograde amnesia in the treated input side only (fig 2). In contrast, cooling of the central processing neuropile (mushroom bodies) initiates retrograde amnesia with a longer time course which is similar to that caused by cooling the whole insect, and the effect is not limited to the treated side of the brain (Menzel *et al*, 1974; Erber *et al*, 1980).

The model arising from these results localizes the specific associative components of the olfactory memory trace in a prominent structure of the insect brain, the mushroom bodies, and the nonassociative memory in the antennal lobes (sensory components) with its direct connections to the suboesophageal ganglion (SOG), where the motor components are localized (fig 3). Such a model is supported by findings on structural brain mutants of *Drosophila*: mutants with distorted or miniature mushroom bodies are able to orient normally to olfactory stimuli, but lack the capacity for olfactory learning (Heisenberg *et al*, 1985). Because the reflex pathway of the PER in bees is based on a direct connection between sucrose receptors on the antenna and motoneurons which run *via* the antennal lobes and the SOG, the neurons connecting the mushroom bodies run parallel to the reflex pathway. Consequently, associative memory does not appear to be a property of the reflex pathway, but rather of a parallel pathway. Therefore, nonassociative (sensitization) and associative memory components may be separat-

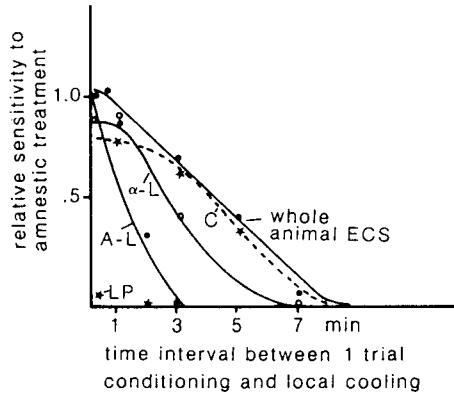
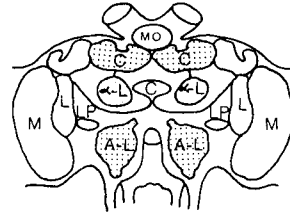


Fig 2. Time courses of the retrograde amnestic effects induced by local cooling of different brain structures after a single olfactory conditioning trial. The insects were conditioned at time zero, and the cooling of the respective structures was performed at the time intervals indicated on the abscissa. Cooling (1–5 °C) lasted only for a few s. The insects were tested for their response to the CS \geq 20 min later. Four paired structures were cooled selectively, the antennal lobes (A – L), the calyces of the mushroom bodies (C), the α -lobes of the mushroom bodies (α -L) and the lateral protocerebral regions (LP). Cooling of the LP did not induce an amnestic effect. However, this does not exclude the possibility that the output regions in the LP are involved in memory processing and storage, because the protocerebral output neuropile lies deep in the brain and may not be reached by local cooling from the front. The time courses for the other 3 brain regions differed markedly. Cooling of the entire insect induced a time course of retrograde amnesia very similar to that induced by cooling the calyces (after Menzel *et al*, 1991). L: lobula; M: medulla; Mo: median ocellus.

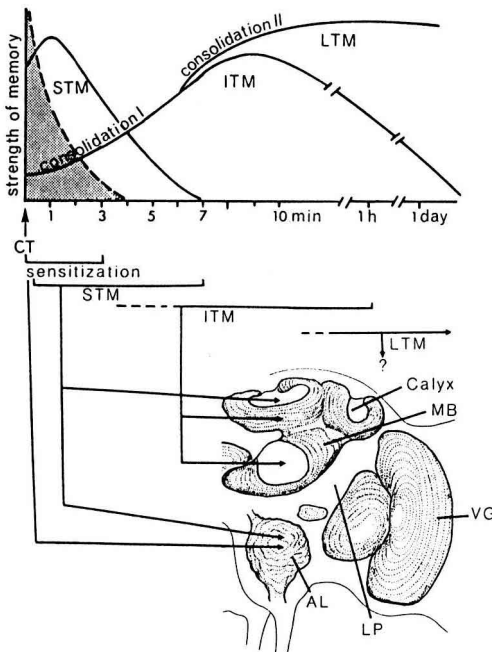


Fig 3. A model of the memory dynamics and localization in the bee brain. The shaded area in the upper graph indicates the non-associative memory induced by the sensitizing effect of the sucrose stimulus (US) alone. STM: short-term memory; ITM: intermediate-term memory; LTM: long-term memory; CT: conditioning trial (at time zero); MB: mushroom body; AL: antennal lobe; LP: lateral protocerebrum; VG: visual ganglia (medulla, lobula).

ed into 2 parallel structures (Menzel *et al*, 1991).

LOCALIZATION OF MEMORY

The concept of functionally and anatomically separated memory traces is supported by single cell recordings. Sucrose (US) induces sensitization effects in neurons at all levels, *eg* intrinsic antennal lobe neurons, relay neurons to the mushroom lobes, projection neurons from the mush-

room bodies to the ganglia in the ventral cord, SOG neurons, intrinsic premotor and motorneurons. Correlates of associative memory are found in neurons downstream from the neurons of the central brain. Mushroom body extrinsic neurons have some properties which are compatible with the neural plasticity underlying associative learning. They are multimodal, have long-lasting stimulus after-effects which outlive a stimulus by many seconds and change their response properties in an associative learning situation (Erber *et al*, 1987). Recently, a single mushroom body extrinsic neuron, the PE1 neuron, has been characterized in great detail. It changes its response behavior to a forward-paired odor but not to a backward-paired odor during differential conditioning (Mauelshagen, 1990, 1993). Thus, specific properties of associative learning are represented at the level of a single identified neuron, the PE1 neuron. These results can be used to support the notion that the mushroom bodies are specifically involved in associative learning. However, it was found that the response changes induced in the PE1 by forward pairing of an odor with sucrose stimulation does not last longer than a few minutes. Since memory lasts for days, it is tempting to conclude that the neural substrate of memory is restructured in such a way that brain regions other than the mushroom bodies (*eg* the lateral protocerebrum) are involved in storing the long-term memory trace. Another possibility may be that the neural circuitry intrinsic to the mushroom bodies may be restructured in such a way that other extrinsic neurons become responsible for the retrieval of the memory.

CONCLUSIONS

The effective learning behavior of honey bees in the context of feeding and the

clear separation between memory processes have helped us to approach basic questions in memory research. The results on the location of the olfactory memory engram in the bee brain provides a working hypothesis, which localizes different forms of behavioral plasticities and the sequential memory phases in different regions of the brain. In essence, the hypothesis states that transient and non-associatively modifiable pathways run parallel to pathways modified by associative learning processes. Pathways, including the mushroom bodies, are considered to change their properties, specifically during associative memory formation, whereas direct connections between the sensory-motor centers or the sensory neuropile of the antennal lobes alone do not contain all the necessary components for an associative memory trace.

Over many decades research on honey bees has contributed substantially to the solution of basic problems of ethology, sensory physiology and neurophysiology, quite apart from the important contributions it has made to sociobiology, ecology and genetics. It is hoped that the methodological advances in neurophysiology and biochemistry will even further increase the importance of this fascinating species for neurobiological research.

Résumé — L'apprentissage associatif chez l'abeille, *Apis mellifera* L. Une vue d'ensemble du comportement d'apprentissage des abeilles est présentée dans le cadre du comportement de butinage. Deux types d'apprentissage sont distingués : l'apprentissage latent (ou par observation) et l'apprentissage associatif. L'apprentissage latent, dont les mécanismes sont encore très mal connus, joue un rôle important dans l'orientation spatiale et la communication par les danses. Il n'y a pas de rapport spatio-temporel avec des stimuli de récom-

pense. En particulier, aucune dépendance quantitative des caractéristiques d'un éventuel stimulus externe de récompense n'a pu encore être mise en évidence pour cette forme d'apprentissage. Une série de paradigmes bien établis a été utilisée pour étudier le conditionnement opérant d'abeilles volant librement et le conditionnement classique d'abeilles immobilisées. Le conditionnement olfactif d'abeilles immobilisées est une méthode particulièrement utile pour suivre la formation de la mémoire à long terme. Elle montre que la mémoire passe par des phases séquentielles qui se différencient par leur sensibilité à la perturbation et la contribution de différentes régions du cerveau. Nos connaissances actuelles sont résumées dans un modèle (fig 3), qui suppose que les composantes fortement non associatives, qui émanent du stimulus inconditionnel (solution sucrée), déterminent la première phase de mémorisation et sont principalement localisées dans le lobe antennaire. Les phases de mémorisation associative se distinguent par leur sensibilité à l'amnésie et par le rôle que jouent les actes répétés d'apprentissage. La phase sensible à la perturbation est principalement attribuée aux corps pédonculés. On suppose que le protocérébron latéral participe également à la mémoire stable, à long terme. L'organisation et la localisation de la mémoire de longue durée sont particulièrement incertaines. Les résultats présentés montrent que l'abeille convient à merveille aux études qui visent à expliquer les bases neuronales de l'apprentissage et de la mémoire.

***Apis mellifera* L / apprentissage / conditionnement olfactif / mémoire / protocérébron / corps pédonculés**

Zusammenfassung — Assoziatives Lernen bei Honigbienen. Das Lernverhalten von Bienen im Kontext ihres Futter-

Sammelverhaltens wird übersichtsartig dargestellt. Zwei generelle Formen von Lernen werden unterschieden: Das latente (oder beobachtende) Lernen und das assoziative Lernen. Für das beobachtende Lernen sind die Mechanismen noch recht wenig bekannt. Es spielt bei der Raumorientierung und bei der Tanzkommunikation eine wichtige Rolle. Ein strenger zeitlich-räumlicher Bezug zu belohnenden Stimuli besteht nicht. Insbesondere wurde für diese Form des Lernens noch keine quantitative Abhängigkeit von den Eigenschaften eines möglichen externen belohnenden Stimulus nachgewiesen. Das assoziative Lernen wurde dagegen sehr genau untersucht. Eine Reihe von Standardprozeduren wurden verwendet, um das operante Lernen von frei fliegenden Tieren und die klassische Konditionierung von fixierten Tieren zu studieren. Vor allem die olfaktorische Konditionierung von fixierten Tieren erwies sich als sehr hilfreiche Prozedur, um die Bildung eines langzeitigen Gedächtnisses zu verfolgen. Es zeigte sich, daß das Gedächtnis sequentielle Phasen durchläuft, die sich hinsichtlich ihrer Störanfälligkeit und der Beteiligung verschiedener Regionen im Gehirn unterscheiden. Unsere bisherige Kenntnis wird in einem Modell zusammengefaßt (Abb 3) das annimmt, daß die starken nicht assoziativen Komponenten, die vom unkonditionierten Stimulus (Zuckerlösung) ausgehen, die früheste Gedächtnisphase bestimmen und vorwiegend in den Antennalloben lokalisiert sind. Die assoziative Gedächtnisphasen unterscheiden sich in ihrer Empfindlichkeit für amnestische Einwirkungen und der Rolle, die wiederholte Lernakte spielen. Die störanfällige Phase wird bevorzugt den Pilzkörpern zugeschrieben. Für die stabile, langzeitige Gedächtnisphase wird eine zusätzliche Beteiligung des lateralen Protocerebrums angenommen. Besonders unsicher ist die Organisation und Lokalisation des langandauernden

Gedächtnisses. Die dargestellten Ergebnisse zeigen, daß die Honigbiene sich ausgezeichnet für Studien eignet, die auf die Aufklärung der neuronalen Grundlagen von Lernen und Gedächtnis zielen.

Lernen / olfaktorische Konditionierung / Gedächtnis / Protocerebrum / Pilzkörper

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