13 - Short-term memory in bees

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Memory as a result of associative learning is not established in its final form immediately after an association has taken place, but needs time to develop. During this time, the hypothetical memory trace changes its properties, and these changes relate to measurable behavioral patterns. For example, the retrievability of the sensory signals involved differs in tests made shortly after learning or later; the effect of newly learned information or the frequency of repetition of the same learning trial changes over time following the initial learning; forgetting has time courses that are thought to reflect different physiological states of the hypothetical memory trace.

The study of the time dependence of memory has been burdened by the controversy whether there is a dichotomy of learning phases (short-term vs. long-term memory) or whether memory formation is a continuous process leading to long-term memory without obvious time phases. I want to stress the point that even if one does not accept the notion of short-term and long-term memory, the undoubtedly different qualities of memory at various times after learning has to be explained. Furthermore, the time dependence of learning and retrieval may be a powerful tool in behavioral studies of learning and may help to characterize the physiological basis of the hypothetical memory trace.

Evidence for a hypothetical short-term processing of information comes from three major sources: human verbal memory studies, studies of experimentally induced amnesia, and chronic disturbances of memory in humans as they appear in psychiatric clinics. It is well documented by now that both for humans and animals the time phases and the properties of the memories for the different paradigms do not fit together at all (e.g., Weiskrantz 1970). Even within one class of experiments as, for example, in studies of induced amnesia, and for just one animal species, the time course of the short-term process may depend on seemingly small differences in procedure. It has been argued, therefore, that the actual time course of short-term processing and storage has very little or nothing to do with basic physiological mechanisms underlying the establishment of a long-term memory trace. Indeed, a hypothesis that correlates the temporal phases of memory directly with different substrates of neuronal activity is much too simplistic for most of the learning tasks used so far to characterize memory phases. Nevertheless, the fact remains that memory formation takes time and has qualitatively different properties at various times.
after learning. Although there is large variation in experimental results, this seems to be a general feature of associative learning processes, at least those that involve relatively complicated motor responses.

Interestingly, there are very few examples of temporal analysis of the retention of a simple conditioned response. If it is true that the temporal phases of memory formation are the result of retrieval mechanisms reflecting mainly changes in motivation and/or attention but not physiological conditions of the memory trace, one should find less obvious changes and no temporal phases in simple conditioned reflexes. I want to apply an even more radical approach. By selecting an insect, we want to reduce the complexity of behavioral studies and prepare for a neural analysis. In addition, if there is any evidence for a short-term phase of memory, the comparison of its properties with those of short-term memory in mammals should be very interesting. From this point of view we ought to examine especially (1) the time course of retention, (2) sensitivity to interference with newly learned information, (3) storage capacity, (4) modes of transfer to a long-term memory, and (5) localization of a labile, short-term memory in the brain.

**BIOLOGICAL BACKGROUND**

Honeybees learn quickly and efficiently to use external signals as reference marks on their food-collecting flights. On the first flight from the hive, they learn the location of the colony with respect to the surrounding landmarks and relative to the sun compass. They learn the color, shape, and odor of the hive entrance. On lengthening excursions during the following several days, they learn landmarks further away and use them for relocating the colony and for adjusting their astronomical compass. When a forager bee flies out to collect nectar and pollen from flowers, it learns the direction and distance of the food source, the landmarks that guide it toward the food source, and the signals of the food source itself: color, shape, odor, and distance from immediate surrounding landmarks (see Frisch 1967). These signals of the food source are learned very quickly: natural odors within 1 trial (Lindauer 1970; Koltermann 1973; Lauer and Lindauer 1973), colors within 1–5 trials depending on the color (Menzel 1968), black and white patterns within 5–20 trials (Wehner & Lindauer 1966, Wehner 1981). The honeybee is able to select the learned food source with extreme accuracy, because each bee is continuously informed about the food supply in the surroundings by the dances of its hivemates and the food spreading within the colony. This means that the individual bee does not have continuously to explore to find out if it is still working (i.e., collecting food) in the most economical way, as do other flower-visiting insects. Both under natural conditions and in behavioral tests, bees choose a food source out of two or more alternatives with more than 90 percent accuracy. Pollen-collecting bees, for example, carry a protocol of their choice behavior with them. Less than 10 percent of the pollen load contains more than one kind of pollen grains, proving that bees select one flower out of many with high accuracy.

Besides the rapidity of their learning and the accuracy of their choices, bees offer other advantages for behavioral tests: (1) low genetic variation, because all test animals are sisters within the same colony; (2) test animals are about
equal in age and in the same behavioral status (forager); (3) they arrive at the
training station in a highly motivated state; (4) new and naive test animals may
be recruited by the dances of previously trained test animals; (5) nonreinforce-
ment in the tests has little if any effect on choice behaviors if the tests are not
continued too long; (6) one animal can easily make 2000 choices a day or more
than 30,000 in its lifetime.

TRAINING PROCEDURES

Karl von Frisch and his coworkers have worked out methods of training indi-
vidually marked bees to come to a feeding station and of measuring their choice
behavior in test situations (see Frisch 1967). In our experiments, the procedure
was simplified by (1) working always with a single test bee at a time, and (2)
testing the choice behavior of the bee with only two alternatives, one being the
learned signal, the other an alternative signal of the same modality. The experi-
ment began with the training of a group of five to eight bees to fly from the
hive to the experimental situation by slowly moving a feeding station step by
step over the 50- to 120-m distance. The experimental situation is a round table
under which there is a light source that projects spectral colors on three ground
glass disks on the surface of the table. The ground glass in the center contains
sugar water and is visible to the bees during training only; the two others,
equally distant from the center, have no sugar solution and are displayed only
during tests. The group of marked bees recruit newcomers, each of which is
then marked as a test bee and rewarded three times on the unilluminated
ground glass. After each reward, the bee returns to its colony. During this
period of time, the group of recruiting bees is captured and kept in a box until
the experiment with the test bee is finished. During the initial three rewards
(pretraining), the test bee becomes familiar with the distance and location of
the feeding station and is motivated to search for food in the center of the table
and the immediate surroundings. After the pretraining, the test bee views the
two colors to be used as discriminative learning signals and is asked about its
preference in a test of spontaneous choice. Spectral colors of equal brightness
for the bee are used (Menzel 1967). After the 4-min test, the bee is rewarded
on one of the colors (λA). The alternative color λA in the test is the comple-
mentary color in all experiments described below. An acquisition function (Fig-
ure 13.1) is plotted by inserting a 4-min test period before each of a succession
of rewards. Acquisition depends heavily on λA, not at all on λA if the two colors
are discriminable for the bee, and very little on the brightness of the colors if
brightness is at least half a log unit above the threshold of the colors (Menzel
1967). Furthermore, acquisition in the first six trials is independent of the
amount of sugar reward (Menzel and Erber 1972), and the same acquisition
function is found if bees are rewarded several times during one visit, with each
landing and sucking counted as a separate reward (Menzel 1968). The acqui-
sition functions mark the genetic boundaries of learning in bees (Menzel et al.
1974). Violet as a food signal is learned fastest, bluish green slowest. Blue (444
nm), the color signal used in most of the experiments described below, is chosen
about 75 percent of the time after one reward.

A different conditioning procedure was introduced by Kuwabara (1957) and
Figure 13.1. Acquisition functions for eight individual bees. The abscissa gives the number of rewards on $\lambda_+$, the rewarded color (532 nm). Choice reaction is expressed in percentage of responses to $\lambda_+$ relative to the responses to $\lambda_-$, the alternative color (413 nm) during the 4-min test situation. The 0 on the abscissa indicates the spontaneous choice test (see text).

has turned out to be extremely useful in studying the physiological basis of learning in bees. Foragers caught at the hive entrance are mounted individually in small tubes (Figure 13.2). Touching the antennae with sugar solution releases a reflex motor program in which both antennae are coordinately directed forward, the mandibles are opened, and the proboscis is extended. This motor pattern can be conditioned to an olfactory stimulus as a conditioned stimulus (CS) (Vareschi 1971; Masuhr and Menzel 1972; Menzel et al. 1974). If a flowery odor is used as the CS, a single conditioning trial changes the response level from about 10 percent (spontaneous response rate) to $\geq 85$ percent. Color signals as CSs are much less effective (Kuwabara 1957; Masuhr and Menzel 1972). Only a third of the bees can be conditioned, and acquisition is very slow.

The true associative nature of the learning process has been demonstrated in terms of all the usual criteria, including stimulus specificity, the role of repetition, the necessity for temporal association between the stimuli and the motor action involved, and long retention (Menzel et al. 1974; Bitterman et al. 1983). For our purposes here, it is important to bear in mind that a single learning trial produces $\geq 85$ percent correct choice in an odor conditioning
experiment when one of two floral-type odors is rewarded and to about 75 percent in a color conditioning experiment with, for example, blue rewarded and yellow as the alternative. This highly significant change in behavior occurs both in free-flying bees and in bees glued to a stage for conditioning of proboscis reflex with an odor as the conditioned stimulus. In all of the experiments discussed in the following, this one-trial learning paradigm was used.

SENSORY MEMORY (STIMULUS TRACE OF CS)

The first experiment demonstrates the existence of a stimulus trace of CS and also includes a control for contingency of CS and unconditioned stimulus/unconditioned response (US/UR) (Figure 13.3) (Menzel 1968). A free-flying bee approaches a spot where it has been fed on several previous occasions. For the first time, the feeding place is illuminated with blue (444-nm) or yellow (590-nm) light, which is switched off 10 sec or 4 sec or 2 sec before the bee lands and takes the reward (left side of Figure 13.3). In another series of experiments (right side of Figure 13.3) the bee approaches the unilluminated feeding place and the color is switched on at the moment of landing, or 2, 4, or 10 sec later. In all cases, the bee sucks sugar water for 30 sec and then flies back to the hive. When the bee returns from the hive, its choice behavior is measured with the two colors (no reward during the test) that were equally preferred if no training is given. The four curves in Figure 13.3 are averages from many individually tested bees. The results show that color is associated with the sugar
Figure 13.3. Two series of experiments that prove the existence of a stimulus trace of CS. Left side (upper bars and open symbols): The color (blue 444 nm or yellow 590 nm) is seen by the approaching bee and switched off 10, 3, or 2 sec before landing and beginning of sucking (+10, +3, +2 sec). This was achieved by observing an approaching bee and switching off the color at some arbitrary time. The interval between this moment and the landing was measured, and the bees were pooled in three groups (12 to 7 sec for the 10-sec group, 4 to 2.5 sec for the 3-sec group, 2.5 to 1.5 sec for the 2-sec group). The bee was fed sugar water for 30 sec, and its choice behavior was tested when it came back from the hive. Right side: The bees approached an unilluminated disk. The color was switched on immediately at 2.5, or 10 sec after landing and beginning of sucking. After termination of sucking the bees viewed the color on their flight off to the hive. As in the other tests, the bees were tested after their return from the hive.

water reward even if it is not seen by the bee for 2–3 sec before reward. A color that is shown only after landing and beginning of feeding is not learned. We conclude from this kind of experiment that (1) bees associate a color as a food signal only when they see it during approach and at the very beginning of feeding—the same was found by Oppinger (1931) and Grossmann (1970); and (2) bees have a sensory memory for color in the range of 2–3 sec.

In other experiments it has been shown that even a very brief reward (as little as a fraction of a second) is sufficient to produce a highly significant change in the choice behavior (Menzel 1968; Erber 1975a). This means that the process of association can go on in a few seconds, including a 2–3 sec sensory memory.
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![Graph](image)

Figure 13.4. Time dependence of retention for free-flying bees trained to a color (long-dashes and closed circles; $\lambda_+ = 444$ nm, $\lambda_- = 590$ nm) and fixed bees conditioned to an odor (orange) (short-dashes and open circles) (Meece and Menzel 1982). Note the log scale of the time axis (abscissa). The outer ordinate gives the percentage of correct choices of free-flying bees, the inner ordinate the responses (proboscis extension) of fixed bees after one conditioning trial (see text).

**RETENTION**

One way to look for transitional periods in the memory trace is to test retention at various times after the learning trial (Figure 13.4). We have done this both for freely flying bees conditioned to colors and fixed bees conditioned to odors. Note that the time is given in a logarithmic scale on the abscissa in Figure 13.4. Retention is best immediately after the one-trial learning, declines in the next 2–3 min, and then slowly increases over the next 10–20 min. After a single trial, retention declines to the spontaneous level of 50 percent within the next 3–5 days, but after as many as three rewards memory is stable for a lifetime of a couple of weeks.

Such a function reminds us of the so-called primacy and recency effects in human verbal learning, where it is found that items encountered first and last are better recalled than the middle items (Weiskrantz 1970). On the basis of such findings it was hypothesized (e.g., Waugh and Norman 1965) that at any instant of time retention will be a joint function of the strength of a short-term and that of a long-term process. If this is the case, the hypothetical short-term memory in the bee should be in the range of few minutes. There is evidence for such an interpretation from experiments with experimentally induced amnesia, but before I describe these experiments I want to report another series
Figure 13.5. Experimental procedure of an experiment that tested the influence of newly learned, controversial information on an initially learned information. Pre, pre-conditioning by three rewards on a grey disk; Sp, spontaneous choice test; 1. blue, first reward on blue; ITI, intertrial interval; 2. yel, second reward on yellow; 1. TA, first session (A) of first test; 1. TB, second session (B) of first test; 3. yel, third reward on yellow; 2. TA, first session (A) of second test; 2. TB, second session (B) of second test.

Figure 13.6. The influence of the time interval (ITI) between two learning trials on two different colors (blue and yellow). See procedure in Figure 13.5. The arrows on the right side indicate the response levels after one reward on blue (1. blue); one reward on blue and one reward on yellow (1. blue, 2. yellow); spontaneous choice level of the two colors blue and yellow (Sp); first reward on blue, second and third rewards on yellow (1. blue, 2. yellow, 3. yellow); and one reward on yellow only (1. yellow). 1. and 2. test – see Figure 13.5. Circles are used to illustrate experiments with 5-sec reward durations, triangles represent experiments with 15-sec reward durations.

of experiments in which we examined the effects of new and contradictory information on recently stored information.

INTERFERENCE WITH NEWLY LEARNED INFORMATION

A freely flying bee learns first the color blue (Figure 13.5) in a single trial and then, after a varying interval of 10 sec to 10 min, the color yellow at the same place. In two test sessions, the bee is asked to choose between the blue and the yellow. To look for any recovery effects, the bee is then rewarded once more on yellow and tested again afterward. Figure 13.6 gives the results. Choice
behavior is expressed in percentage choices of blue, and the abscissa gives the interval between the two trials. Except for the very first part of the function, intertrial interval (ITI) ≤ 1 min, the curves have the expected shape if one assumes the resistance of a memory trace to interference from a new learning signal is correlated with the strength of the memory trace: After consolidation, when memory is most stable and most efficient in controlling behavior, it is also most resistant to new and contradictory learned information. Memory seems more labile during the transition from a short-term to a long-term trace. The very early high sensitivity to new information (ITI ≤ 1 min) is more difficult to interpret, and further experiments are needed to determine whether there are any qualitative differences between this part of the function and the others.

It was well known already to Müller and Pilzecker (1900) that recent memory is more sensitive to interference (“retroactive inhibition”) than older memory. It is tempting to speculate that such an “erasing mechanism” may have a neurophysiological basis, as was recently argued by Krasne (1976).

**EXPERIMENTALLY INDUCED AMNESIA**

A strong retrograde amnesic effect is caused in both freely flying color-trained bees and in fixed bees conditioned to an odor by electroconvulsive shock (ECS), cooling to +1°C, and narcosis with CO₂ or N₂ shortly after learning. Details of the experimental procedure can be found in Menzel (1968), Erber (1976), and Menzel et al. (1974). Figure 13.7 gives the results for bees conditioned to blue in one trial. Treatment immediately after the trial has the strongest effect: at an interval of > 5 min the choice behavior is not different from a control (B in Figure 13.7), which was sham-treated and then tested more than 15 min after conditioning, as were all the other animals. Another control group (C in Figure 13.7) served to determine whether the ECS acts as a negative reinforcer. Bees were ECS-treated after they had landed on blue but without being conditioned, and their choice behavior was tested afterward. On the average, they chose the blue at the same frequency as untreated animals (50 percent).

I want to emphasize that in these experiments freely flying bees came back from the hive when they were motivated to search for food. Therefore, two arguments suggested most frequently against EC experiments do not apply here: The motivational state is not changed, and the treatment does not cause some sort of counterconditioning.

The four treatments used differ in the time courses of their amnesic effects, perhaps because the different speeds with which they affect the bee: ECS acts immediately, causing convulsions from which the bee recovers within the next 5–10 min. Cooling takes 1.5–2.0 min before the bees no longer react to stimulation. Besides these temporal effects, however, there may be additional effects that we have not yet studied in detail.

It is tempting to argue that recent events are in a qualitatively different neuronal state than those more distant events that are untouched by ECS. In a popular view, this early state is called short-term memory (STM), and it is argued that there is a gradual autonomous transfer from short-term storage to permanent storage (long-term memory, LTM). What defines this gradual transfer to long-term storage? Is it simply the time dependency of an internal,
autonomous process? Is the transfer a gradual progression from STM to LTM? These are basic questions of memory research that can be addressed experimentally in bees. There is ample knowledge from studies of humans and of laboratory mammals that the serial progression assumption is very unlikely and that time dependency alone does not explain the various experimental data (Weiskrantz 1970). But how about such a "primitive" creature as the bee with its little brain, less than a millionth of the size of the human brain?

Time dependency may be a more crucial factor in the bee because we find very similar time courses in the two experimental paradigms we have used so far, the freely flying color-learning bee and the fixed odor-conditioned bee. A closer analysis reveals, however, that in the bee, too, time dependency is just one factor; parallel processing and immediate access to long-term memory are others.
Figure 13.8. The effect of ECS on massed training trials. The first three pairs of bars give the choice reaction after one, two, and three training trials (1R, 2R, 3R) in comparison with always one more training trial plus immediate application of ECS (2R + ECS, 3R + ECS, 4R + ECS). Choice reaction is equal in experiments with x number of training trials and x-1 numbers of training trials plus immediate ECS. If ECS is applied 7 min after the training trials (see right pair of bars, 2R + ECS), no effect of ECS is seen.

Erber (1975a, b) has studied these questions by combining massed trials with ECS treatment. The results in Figure 13.8 are twofold. First it is shown that a 2-sec reward causes the same change of behavior as a 30-sec reward. Then it is found that an ECS treatment immediately applied after two, three, or five short (2-sec) rewards within less than 30 sec eliminates only the learning effect of only one learning trial: Choice behavior is similar in bees trained with nE rewards plus immediate ECS and in bees trained by nE - 1 rewards without ECS. Figure 13.8 shows another control: if ECS is applied 7 min after the series rewards, choice behavior is similar to that of bees without ECS treatment.

As Erber (1975b) pointed out, there are two possible explanations to his findings: Either (1) there is direct access to LTM if the hypothetically limited STM capacity is occupied; or (2) there is a speed-up of transfer from short- to long-term memory in massed trials. To test these alternatives, a preliminary experiment was carried out by conditioning fixed bees to two different odors shortly after each other, one trial with each odor. Immediately afterward, the bees were cooled to +5°C. The results so far are in agreement with the second interpretation, indicating a limited storage capacity of STM. It is tempting to speculate, as has been done for verbal items in humans (Müller and Pilzecker 1900; Miller 1956; Peterson and Peterson 1959; Weiskrantz 1970) and for various conditioning treatments of laboratory mammals, that the transfer from a limited-capacity short-term store to a long-term store is dependent both on time and information flow. The result is that under certain conditions long-term storage is reached nearly immediately, giving the impression of parallel
NEURAL STRUCTURES INVOLVED IN STM–LTM TRANSFER

Experiments of the kind I have described so far aim at a more direct analysis of the brain mechanisms underlying learning and memory. The goal is to relate brain events with behavior, in particular the change of behavior as a result of experience. We wish to find the neural substrate of the change in behavior, as opposed to the substrate of the behavior per se. The paradigms used must permit one to distinguish between neurophysiological substrates of learning and performance. There must be changes that develop within the brain system involved in learning and memory. How do we search for the location of these brain systems?

Brain lesions are inappropriate methods, as we know from many studies (e.g., Hebb 1949), but if one could locally and temporally bind the transient destructive effect on the short-term store, one might get information on the participation of certain brain areas in the establishment of long-term memory. We have used local cooling immediately after one-trial learning of an odor signal to probe various structures in the bee brain (Masuhr and Menzel 1972; Menzel et al. 1974).

As you may suspect, the bee brain is relatively small, so the cooled pencil has to be sharpened before use. Actually, the bee brain, more accurately the suprasophageal ganglion, has a volume of about 1 mm³ and contains about 900,000 neurons. About 80 percent of the neurons are in the two large optic lobes. The midbrain is dominated by a paired neuropil of densely packed neurons, the corpora pedunculata or mushroom bodies. These mushroom bodies have been suspected to be the center of intelligence in bees for a long time (von Alten 1910). This suggestion is supported by the structural regularity of the globula fibers, the input from olfactory and visual centers, and the extreme high density of fibers and synaptic connections (Schürmann 1970, 1972; Mobbs 1982). Each mushroom body is divided in two caplike structures (the calyces) connected by two short fused stalks (pedunculus) and two lobes (α- and β-lobe). The input regions are the calyces, the output regions, the pedunculus, and the α- and β-lobes. Figure 13.9 shows in addition the outline of the pair of lobulae, the third visual neuropil, and the pair of antennal lobes, the sensory neuropil of the antennae. Primary sensory projections from the antennae reach the antennal lobes, the subsophageal ganglion, and a region caudal to the antennal lobes. Secondary olfactory neurons connect strictly ipsilaterally the antennal lobes with the calyces and two regions in the lateral protocerebrum. Note the circular arrangements and length of the secondary olfactory neurons. For local cooling, we have used one or two needles with a tip diameter of 150 μm cooled to +1°C. The main results of these experiments are given in Figure 13.9. The shaded circles show the areas cooled for a short period of time (2–5 sec). In all three experimental series considered here, both antennae received the odor signal and both paired structures were cooled.

The cooling effect is limited to a period of a few minutes after the one-trial learning. Cooling the antennal lobes later than 2 min, the α-lobes later than 3–
Figure 13.9. The effect of local cooling of small brain regions during the transition from short- to long-term memory. Left: Outlines of some brain structures. A. Lobus, antennal lobe (sensory neuropil of the antennae); I. Prot., lateral protocerebrum; α-Lobus and Calyx, two parts of the mushroom bodies (corpora pedunculata); Oc, ocelli; UG, subesophageal ganglion. The thick lines indicate the primary (into antennal lobe and subesophageal ganglion) and secondary projections from the antennal nerve (see text). Right: Time courses for the cooling effect in three brain areas. In all three cases both structures in the left and right hemisphere of the brain were cooled for a few seconds. The dashed line in the bottom figure gives the time course for cooling the whole animal. (For details see text and Erber et al. 1980.)

4 min, and the calyces later than 5 min after learning cause no reduction of response in a test 15 min later. Blockage of the transfer to a permanent store, therefore, is caused only if the sensory integration centers (antennal lobes) are cooled shortly after the learning trial. For both compartments of the mushroom body, the susceptibility to cooling is considerably longer, and the time course for the calyces is very similar to that of cooling the whole animal (dashed line), although only the two frontal calyces of those on either side have been cooled. No reduced responsiveness was found when the lateral protocerebrum close to the lobula area was cooled.

We conclude from these experiments, which have been performed with various permutations of parameters and a number of controls: (1) A circulating
neural activity between antennal lobes, mushroom bodies, and lateral protocerebrum is not the substrate for STM. Vowles (1961, 1964) formulated such a hypothesis on the basis of the striking circular feature of the second-order olfactory neurons and lesion experiments; (2) STM is not localized in a limited area of synaptic interaction – instead, several widespread neuropiles take part, although with different time courses.

More generally, with these experiments we have found another surprising parallel relationship to memory in mammals, namely the participation of several widespread neural structures in the initial memory process. Our data do not allow us to separate between the possibility of several memory traces, as Hebb (1949) argued, or of one trace changing its property over time differently in the participating structures. What our data exclude definitely, however, is the possibility of a unique synaptic focus for the changes that occur when the bee learns to associate a specific odor with food reward.

In summary, short-term memory in bees is characterized by (1) a maximal duration of a few minutes, as seen in retrograde amnesia experiments; (2) its precise control of behavior; (3) its initially high sensitivity to interference from new learning; (4) its limited capacity; (5) its rapid transfer to long-term memory under conditions of high information flow; and (6) its widespread representation in the brain. Furthermore, (7) STM is preceded by a sensory store. Considering the small brain of the bee, the different structural basis of its neuronal wiring, and the different evolutionary adaptations of its learning system, the parallels with mammalian learning are striking.

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