Memory Traces in Honeybees

Randolf Menzel
Institut für Tierphysiologie, Neurobiologie, Freie Universität Berlin, Königin-Luise-Str. 28–30,
D-1000 Berlin 33, FRG

Abstract. Bees learn quickly and effectively the signals which mark a nectar source. The
memory for these signals (colors, odors) is characterized by behavioral experiments. Four
sequential memory stages - called working memory, early, late and permanent memory - are
found, which differ with respect to their sensitivities to unrewarded choices, to new learning
trials, and to amnestic treatments. The neuropiles in the brain are differentially involved in
the respective memory traces for odor signals. It is concluded that the primary afferent
structure, the antennal lobe, participate only in the working memory phase. The most
important neuropiles for memory formation are the mushroom bodies. The content of the
early and late memory differs for a floral odor, but not for an attractive pheromone
component. Genetic selection for low learning performance reveals bees, which lack the late
memory but are unaffected in the early memory. The results are discussed in relation to the
adaptations of the memory stages to the particular search behaviour of bees at floral
patches.

INTRODUCTION
Honeybees collect nectar and pollen from flowers, not randomly, but with a systematic
search strategy. The most important component of this strategy is the learning behavior of
the individual bee, and the long lasting memory which results from a fast and effective
learning process. If one follows marked bees on their way from one flower to another, it
becomes obvious that the individual bee sticks to one kind of flower, although other species
of flowers in the same area offer nectar at the same time and are visited by other bees (23,
25, 34). Flower constancy - as this behavior is called - has been known for a long time, and is
well documented. One easily accessible document of this is the pollen load carried on the hind
legs of every pollen collecting bee. Inspection indicates that in nearly all bees the pollen
comes from one plant species only (8). Bees observed carrying pollen from 2 - 3 different
species of flowers were later found to sample pollen from only one of these flower species,
and were thus observed initially at that moment when they switched from one plant species
to the next.
Flower constancy requires that the bee not only recognizes the species-specific signals of the flowers but also has the ability to store the signals in a memory which guides the choice behavior in the future. We know from Karl von Frisch's early training experiments (9) that this memory is the result of a learning process in which the flower signals are associated with food reward (19). The learning process follows basic rules of associative learning (1, 15). In addition, associative predispositions and selective associations guide the learning behavior—aspects which shall not be elaborated on here (see 10, 13). The memory is stable and can last for a lifetime, even after a short period of learning. The first report on the stability of memory in bees comes from Lindauer (14), who found that a group of bees searched at the same feeding place after more than 3 months of winter rest. Similarly, I observed that the summer bees did not forget a color signal for 2 weeks, even after only 3 rewards on that color (15).

The aim of this paper is to characterize the memory trace for food signals in honeybees with behavioral experiments. I shall start with observations of the natural, undisturbed choice behavior, and finish with experiments which are designed to locate and manipulate the memory traces in the bee brain. The concept behind these experiments is that an associative learning trial triggers a sequence of automatic memory processes, the neural properties of which are reflected, at least partially, in behavioral and physiological measurements.

The idea of a central nervous automatic memory processor has its roots in the ethological concept that the continuous flow of behavior can be partitioned into components which reflect the operation of elementary mental processes. Such elementary processes are relatively close to the neural mechanics of the brain. Their separation and characterization may tell us something about the neural machinery involved, and thus, may help us to identify more precisely the underlying neuronal mechanisms.

Memory traces are needed at two distinct temporal windows

Under natural conditions bees fly out from the hive many times during a day and visit many flowers during one foraging bout. The time interval between foraging bouts is in the range of several minutes, and the frequency of landings on flowers lies in the range of a few seconds. Examples are given in Fig. 1. Fig. 1a plots the frequency of intervals between bees returning to the hive and successive arrivals at an artificial feeding place about 100 m from the hive. Fig. 1b gives a frequency histogram of intervals between successive choices at four different plants, whose flowers appear in patches. These were the leopard's-bane Doriocum, the orange tree Citrus, the crested jark Corydalis, and the willow Salix. The measurements from the four different plant species have been cumulated because no great differences between species were observed, even though the average distance between the flowers was quite different and the quantity and kind of food (nectar, pollen) offered at each species was also different. It appears from these observations that the memory from former experience is needed at two distinct temporal windows, immediately after a choice (time interval in the range of
seconds), and when the animal returns from the hive (time interval in the range of several to many minutes). Furthermore, a stable, long lasting memory is needed for choice behavior after long intervals (days, weeks and months).

![Graph A: Frequency of intervals between foraging bouts](image)

![Graph B: Frequency of intervals between floral choices](image)

**Fig. 1 - Temporal windows for the choice behavior of honeybees.** a. Frequency of intervals between arrivals at an artificial feeding place 100 m from the hive. Data were collected over 1 week during late summer. b. Frequency of intervals between approaches of flowers in a patch. Individual bees were followed from flower to flower, and intervals between successive landings on flowers were recorded. The flower patches were: Doronicum (1), Citrus (2), Corydalis (3) and Salix (4). n: number of choices at respective flowers (1-4).
The temporal dynamics of the memory trace
When we tried to test the question whether bees apply different kinds of memory for the second, minute and day range, we ran into the problem that the bees learned too fast; after only three learning trials on a blue feeding place a very high proportion of the bees chose blue (90 % correct in a dual choice situation). They retain the memory at the same high level for their life time. Odor trained animals are even more precise; three learning trials change the behavior to 100 % correct choices. However, when free flying bees were trained in only one learning trial to a color signal or fixed bees conditioned by one trial to an odor, we found the following temporal dynamics in a free running recall test: Immediately (up to 2 min) after the learning trial the proportion of correct choices is very high, then it decreases and reaches a minimum at about 3 min, and then learned performance rises again after 4 min, Fig. 2a, b). In this experiment each bee was tested only once at a particular time after the one-trial learning. The time course is the same for free flying bees trained to a color signal and fixed bees conditioned to an odor signal. The improvement of the memory with time without additional learning experience reminds us of memory consolidation in mammals and man (4, 26).

![Graph](image_url)

Fig. 2 - Temporal dependence of choice behavior (a) and of conditioned responding (b) in a free running recall experiment. In (a), the freely flying bees were trained by one trial to blue and tested at various intervals in a dual forced choice test between blue and yellow. The inner scale of the ordinate gives the percentage of choices for blue. (3 refers to the spontaneous choice level at 50%, 1.0 to 100% correct choices of blue). (n = 7.352). In (b), the fixed bees were conditioned with one trial to geraniol and tested for conditioned responses at various intervals. Each of the 240 bees was tested only once. The outer scale of the ordinate gives the percentage of conditioned responses. No bee responded before conditioning (0). (curve a after Ref. 14, curve b after Ref. 21)
After consolidation, memory decays over several days following a one-trial learning. As mentioned above, no memory decay was found when bees were trained in three trials and were not allowed to make any new experience.

A corresponding temporal dynamic of the memory trace can also be seen in other memory tests. Two such tests shall be considered here: (1) sensitivity to a new learning experience, and (2) sensitivity to amnestic treatments.

(1) If free flying bees are trained first to blue and then, after various intervals, to the alternative color yellow, the bees are more resistant to reversal with shorter and longer intervals between the training sessions than with intermediate intervals (Fig. 3a). With very short intervals (less than 1 min) bees reverse to the second color signal also very efficiently. However, this latter effect depends on the duration of the reward; it is not apparent with longer reward durations. Bees conditioned to two odors in succession at intervals of 1 min, 3 min or 10 min, respond to the odor conditioned first equally frequently, but differently to the odor conditioned second: the response is highest at an interval of 3 min, and lower at 1 and 10 min intervals, although the memory tests have been performed 30 min and 90 min after conditioning. Both series of experiments indicate a weak memory trace for the signal learned first at 3 min after the single learning trial, just at the time when the learned behavior is less well under the control of the memory trace (compare Fig. 2 and 3).

As mentioned above, the memory trace immediately after the learning trial (up to 1 min) depends on the reward duration (Fig. 3a), indicating a particular weak memory trace shortly after a small reward. This conclusion is supported by the finding that extinction trials following a one-trial learning of a color signal, weaken the learned behavior more after short rewards than after long rewards (Fig. 4).

(2) The memory trace following a single learning trial also has temporal dynamics with respect to experimental procedures like narcosis, cooling and electric stimulation of the brain (EBS). Erber (5) demonstrated that these procedures cause retrograde amnesia if applied shortly after the learning trial. After the memory trace has been consolidated (more than 5 min after the single learning trial) it is no longer susceptible to interference. Massed learning trials facilitate the consolidation process. If 2, 3 or 4 learning trials follow each other quickly and well within the period of high susceptibility after one trial (within 1 min after the learning trial), only the contribution of one learning trial is erased with e.g. EBS.

The same temporal event processes are found in odor conditioned bees (Fig. 5a) (7, 19, 20). A particularly quick repetition of conditioning trials make the memory trace immune against amnestic treatments. The obvious questions that arise from these findings are: (1) what protects the early memory trace from the amnestic effect - the additional CS (conditioned stimulus) or US (unconditioned stimulus) alone or the pairing of CS and US (an
Fig. 3a - Two trial reversal learning experiment. Individual free flying bees were trained by one trial to a blue target and then after various intervals (intertrial interval ITI, abscissa) to a yellow target by one additional trial. The two colors (blue and yellow) were presented 10 - 30 min later, and the choice behavior of each bee was tested for 4 min. Before training the bees chose the two alternatives nearly equally frequently (dotted line sp). The choice behavior after the two trial reversal learning depends on ITI. Short (5 sec, curve a) and long (15 sec, curve b) reward durations result in different time courses for ITIs of up to 1 min. The two ordinates give the percentage of choices for the yellow target (left side) and for the blue target (right side) in the dual forced choice test. (Curve a: number of animals N = 57, number of choices 1,693; curve b; N = 141, n = 278) (After Ref. 15)

Fig. 3b - Two trial reversal conditioning experiment. The bees were first conditioned by one trial to either carnation or geraniol (O1) and after 1, 3 or 10 min ITI by one trial to geraniol or carnation (O2). The response to geraniol and carnation was tested 30 min later. The sequence of the odors during the tests was balanced by two subgroups each, and the results pooled. Since the kind of odor conditioned (carnation or geraniol) did not matter the groups were pooled. Thus the response value to O1 or O2 includes both odors. The conditioned response to O1 is independent of the subsequent conditioning to O2, but the conditioned response to O2 depends on ITI.
Fig. 4 - The effect of extinction (unrewarded choices) after one long reward (curve a, 15 sec) and after one short reward (curve b, 5 sec). Free flying bees were trained by one reward to a blue target and tested 15 - 30 min later in a dual forced choice test (blue - yellow). (After Ref. 14)

associative trial), (2) is the memory trace of the first learning trial shifted to a stable form more quickly, or does the memory trace of the second learning trial reach the stable form immediately? We found that an additional exposure to the CS or the US alone, prior to EBS or cooling, does not protect the memory trace, but an additional learning trial does protect it, even if a different odor is used in the second learning trial (19). This finding gives us the unique opportunity to address the question of whether the memory trace of the first or the second learning trial reaches the stable memory more quickly. In our experiments, the two different odors (O1 and O2) were carnation and geraniol. Since both odors were used as a first or a second odor, and the data are pooled, in Fig. 5b, we refer to the odors as first or second trained odor (O1 and O2). O1 and O2 were trained in quick succession, and the EBS was applied immediately thereafter (within 30 sec). As Fig. 5b shows, the amnestic effect is restricted to O2. The response level for O1 is not different from that of the control group. (The response level of the control group is different for the first and second conditioned odor. This indicates a so called recency effect, which is well known in the learning literature. This effect shall not be discussed further here.)

We can conclude from these experiments that the memory trace has dynamic properties which depend on time and on associative events. The establishment of a stable memory form is faster with repetitions of associative events (but not just US or CS). After a single associative event the memory requires a much longer time to reach the same stable form. The correction by a new learning trial is more effective within the first minute after the learning trial if the duration of the reward is short, and less effective if it is long. The behavioral consequence of this is that after one learning trial the time period for corrections within the labile memory form is considerably extended and reward dependent, whereas after
**Fig. 5a** - The effect of EBS on memory consolidation. 1 trial: 3 groups of animals (40 in each) were conditioned by one trial to carnation and tested 30 min later. The control group C was sham treated, the 30 sec group was shocked 30 sec after the learning trial, and the 7 min group was shocked 7 min after the learning trial. 3 trials (in 30 sec) two groups of animals (C: 16 animals, 30 sec: 17 animals) were conditioned by 3 trials within 30 sec. The control group (C) was sham treated, the 30 sec group shocked 30 sec after the last learning trial. The animals were tested 30 min later. Control groups: 1: odor paired with EBS. The response level to the odor is not different from untreated animals (n = 14) 2: EBS treatment 10 min prior to conditioning (n = 32) (3 trials). (Compare with the control group of the 3 trials experiment).

**Fig. 5b** - Dual odor conditioning and the effect of EBS. Two groups of bees were conditioned first to odor 1 (O1, carnation or geraniol) and then to odor 2 (O2, geraniol or carnation) by one trial each in quick succession (within 20 sec). The control groups were sham treated (open bars), the experimental groups treated immediately by ECS (hatched bars). The response to the conditioned stimuli O1 and O2 were tested 30 min later. Half the bees of each group were tested first to O1, the other half to O2, and the results pooled. One star (*) indicates significant differences on the level of p 0.05; two stars (**) of p 0.01. (see text). (Courtesy of M. Sugawa).
several learning trials, the response reaches asymptote quickly, is independent of reward duration, and the memory trace is strong and stable.

**Selection for good and bad learners reveals differences in the dynamics of the memory trace**

Recently, Brandes (2) selected bees for their learning ability using the olfactory conditioning paradigm. He isolated good and bad learners and bred them first parthenogenetically and later sexually by internal crosses (see Moritz and Brandes, this vol.). We tested the two lines after 3 generations of separation, in a free running recall test, and found the well known biphasic time course in the good learners with a somewhat speeded-up early memory phase, and a very different time course in the bad learners (Fig. 6). Initially, the bad learners respond equally well to the CS than the good learners, but the memory in the bad learners deteriorates more quickly. Furthermore, the early dynamic properties are reversed in the bad learners, although this effect is not statistically significant in a point to point comparison.

These results remind us of the Drosophila memory mutants dunce, rutabaga and amnesiac (22), which are affected in their ability to establish a long-term memory. Other than in Drosophila, we do not know how many genes are involved and which enzymatic processes are damaged, but we can conclude from these results that the dynamics of the memory trace, following a single learning trial, are under the control of the genome and thus reflect an inherent property of the underlying neural network.

![Graph showing the time course of recall after one trial odor conditioning in bees selected for good and bad learning behavior. Each of the two groups of bees (n=166, n=158) was conditioned once to geraniol and tested once only at varying intervals after conditioning (abscissa).]
The content of the early and late memory trace

So far, we have tried to characterize the conditions which are necessary to establish a stable, long-term memory. Now we want to ask whether the content of the early and late memory trace is the same or different. Again we can approach this question only with indirect behavioral methods. One way is to determine whether the generalization gradient is the same at different times after one learning trial (Fig. 7).

Fig. 7 - Generalization gradient during the early and late memory. Groups of bees trained to pentanal (upper part of the figure, total n = 235, each group: n = 25 or more) or citral (lower part of the figure, total n = 243, each group: n = 30 or more) by one trial. 30 sec (vertical stripes) or 15 min (horizontal stripes) after the conditioning trial the bees were tested by presenting one of four different odors (pentanal, citral, geraniol, 2-pentanol). (See text) (Courtesy of B. Smith).

A group of bees is trained to either pentanal or citral in one conditioning trial, and then tested by 1 of 4 different odors either 30 sec or 15 min after conditioning. It is established beforehand that all 4 odors are well discriminated by the bees if they are differentially conditioned in several trials. After one trial the bees also partially respond to the non-reinforced odors, demonstrating a profile of generalization. It turns out that if the floral odor pentanal is conditioned this profile is significantly different for the early and the late memory trace. This is not so if the pheromone component citral is conditioned. In the case of pentanal, the neural processing underlying the transfer from an early to a late memory trace makes the profile sharper, and thus increases discrimination by some process that we might call "mountain climbing", in analogy to the properties of an associative matrix (24).
"Mountain climbing" might be seen as a process which changes the content of the memory trace by some internal control mechanism (e.g., an autocorrelation of the neural excitation subserving the early memory trace). Such a mechanism may be involved in the consolidation of an unspecified stimulus like a floral odor, which can be one out of very many kinds of odors. In the case of a specified or labelled stimulus, like the component of the Nasanov secretion citral, the final memory content may be reached immediately because the neural structures for such an appetitive association may exist already in a highly prepared form. Learning of labelled stimuli may thus follow the scheme of an alpha-conditioning as discussed by Gould (10), whereas unlabelled stimuli may require a much more flexible and unspecified network with higher self-organizing properties. It is tempting to speculate that the patterns of connections in the brain for prepared associations are the same for the different memory phases, but different for the open or unspecified associations. However, it is important to notice that the time and event dependencies as described above are not different for floral odors and pheromone components.

An attempt to localize the memory trace

The bee brain may be relatively large by insect standards, but it is small (~1 mm across) for the coarse methods which are available for a search for neural correlates of the proposed memory traces. Many of the 950,000 neurons are located in the visual system, which may not concern us in the context of olfactory learning. The prominent structures of the olfactory system are the two antennal lobes, the two mushroom bodies with their double calyces and single alpha and beta-lobes, and the fibre tracts connecting these structures (see Masson, this vol.). The suboesophageal ganglion (SOG), which contains the motoneurons subserving the motor-program of the proboscis extension, receives direct input from the antennal nerve and descending neurons from the deutocerebral and protocerebrum (see Bicker et al., this vol.).

Recordings have been made from the AGT-neurons (13), alpha-lobe extrinsic fibres (11), Kenyon cells (6), motor- and pre-motor neurons in the SOG (see Bicker et al., this vol.). Unfortunately, no clear correlations between neural activity and learning or memory, other than relatively long lasting stimulus after effects (6, see Erber and Homberg this vol.) have been found so far. The search for the memory trace, therefore, is still restricted to the identification of neuropiles possibly involved in the storage process.

In our first attempt we used cold needles (tip diameter 150 μm) to reversibly block neural activity for a few sec at various intervals after one-trial learning (7, 17, 19). Different courses for the retrograde amnestic effect were found for different regions in the brain. If only one antenna was stimulated during conditioning and either the ipsi- or the contralateral neuropile cooled, the participation of the ipsi- or contralateral structure could be observed. It appeared that there is no amnestic effect if the lateral protocerebrum was cooled, a very transient one if the antennal lobes were cooled, but longer lasting effects if the alpha lobes and the calyces were cooled. Although we can not firmly conclude from such experiments
that the process of transfer to a stable memory trace resides in the mushroom bodies, these results indicate that the mushroom bodies are essential structures for the process involved in establishing a stable memory trace over several minutes. Furthermore, neither a reverberating circuit antennal lobe - calyces - lateral protocerebrum - antennal lobe, nor the antennal lobe or the lateral protocerebrum separately are essential for the process. The antennal lobes are involved in the very first period (up to 1 min) after a learning trial. It is thus likely that the antennal lobes are involved in the very first and very sensitive period of the memory trace, but not in the consolidation of the memory.

To appreciate the results after unilateral olfactory stimulation of the antennae and the local cooling of the ipsi- or contralateral structures, a peculiar property of olfactory learning in bees has to be pointed out. If only one antenna is exposed to the odor during conditioning, the bee will respond to that odor only if it is presented to the same antenna and not, if the other antenna is stimulated (19). Does that mean that the memory trace is restricted to the ipsi-lateral side of the brain? Indeed, no contra-lateral cooling effects are seen in the antennal lobes, but the contra-lateral mushroom bodies, particularly the calyces, are involved. Also, the contra-lateral alpha lobe appears to participate in the memory trace, because bi-lateral cooling is much more effective than ipsi-lateral cooling alone. However, contra-lateral cooling in the alpha lobe alone had very little effect in our first experiments (7, 19). We studied this question again with better temporal resolution and higher spatial selectivity (Fig. 8).

![Graph showing the annestic effect of electric stimulation of the alpha lobe. The bees were conditioned once to geraniol by stimulating only one antenna with the odor. EBS was applied to the ipsi- or contralateral alpha-lobe immediately during conditioning, or after intervals of 2 sec, 30 sec, 3 min, 5 min or 10 min. The conditioned response was tested 30 min after the EBS application by stimulating the same antenna with the odor as was done during conditioning. (The bees never responded to the stimulation of the other antenna). (Courtesy M. Sugawara.)](image-url)
In this experiment the amnestic treatment is a weak electric stimulus (ac 100 μA, 50 Hz, pulse duration 1 ms, for 2 sec) applied differentially through 2 microcapillaries at the median and lateral margin of the ipsi- or contra-lateral alpha lobe. There is a normal retrograde amnestic function if the ipsi-lateral lobe is treated. But if the contra-lateral lobe is stimulated we find a bi-phasic function with no amnestic effect during and shortly after the learning trial. It should be emphasized that the tests for an amnestic effect are carried out 30 min after the treatment, and the CS is presented to the same antenna as during the conditioning trial. (If the CS is presented to the other antenna there is never a conditioned response as mentioned above).

It thus appears that localized amnestic treatments focuses our attention on the mushroom bodies as being potential structures subserving the inherent self-organizing process for the establishment of a permanent memory trace.

CONCLUSION
A few associative learning trials can change the behavior of an animal like the honeybee for its life time, a single learning trial for many hours or even days. The learning trial is a very short event. In the honeybee it may last just 3 sec including the full length of the exposure to the CS and US. The changes executed in the brain by such a short event develop over time and under the influence of additional learning trials. The engram or memory trace must, therefore, result from an inherent automatic machinery that is specifically triggered by the associative event and involves internal, self-organizing neural processes. Hebb (12) has used the term "cell assemblies" for these self-organizing, self-instructing groups of neurons, which are assembled temporarily or permanently by the process of learning. It is very likely that a "cell assembly" is in reality composed of many neurons, and that its crucial functions are only incompletely reflected in single members of the group, or the synaptic connection between two members. Cellular neurobiology may have limited access to these crucial functions. We have relied heavily, therefore, on behavioral methods in our attempt to characterize these automatic memory processes. It is obvious, however, that behavioral methods give only indirect and - at the best - suggestive evidence. Neurophysiological approaches are needed for more direct tests of these hypotheses, and these approaches have to built on the cellular neurobiological methods that are used so successfully in learning studies with molluscs.

Our results are consistent with a model that assumes a time and event dependent sequential structure of memory stages. These memory stages are characterized by their time course in free running recall tests, their differential control of choice behavior, their sensitivities towards associative events and retrograde amnestic treatments, their distribution in the brain and their separation by genetic selection. Furthermore, the memory content may be different in the early and late memory stages.
Nothing is known so far about the neural and cellular mechanisms underlying the memory phases. The enormous speed-up by additional associative events indicates that the slow process of consolidation after a single learning trial may not be limited by metabolic restraints, but is rather an actively retarded process that exposes the recently learned information to additional controls before a permanent trace is established. It is conceivable that the same critical substance (e.g., a second messenger like cAMP) is synthesized very slowly after a single trial and very rapidly after massed trials, and that the consolidation into a late and permanent memory may depend on the concentration of just this substance at critical locations within the "neural assembly".

The experiments reported here suggest a sequence of 4 memory stages following a single associative learning trial:

1. a working memory lasting up to 1 min, which controls learned behavior very well, is sensitive to reward duration, to extinction trials, to reversal learning, to amnestic treatments, and which resides in the ipsi-lateral brain including the antennal lobe; 2. an early memory, which initially controls learned behavior very well, but also loses this ability quickly (within 2 -3 min), is less sensitive to extinction, reward duration and reversal learning. It can be erased by amnestic treatments. Bees genetically selected for low learning performance are not affected in the early memory. The mushroom bodies in both sides of the brain take part in this memory trace. 3. A late memory, which develops over time after 4 min following the learning trial, gains increasing control over learned behavior with time (consolidation) and becomes more resistant to reversal learning. Late memory deteriorates after more than 12 hours. It is insensitive to amnestic treatment, and is absent in animals selected for low learning performance. The localization of the late memory trace in the brain is unknown, but most likely involves both mushroom bodies. 4. a permanent memory, which is established only after more than one learning trial, is stable for the life time of the animal and is changed only by new learning trials.

A multiple memory trace system is not a unique feature of the bee brain. However, the actual temporal dynamics and the particular qualitative and quantitative properties are adaptations of the species to the general pattern of food encounters under natural conditions. The sequence of the memory phases after one learning trial ensures that the initially stored information is transferred to a lasting memory only if it is reinforced by additional learning trials, or by an extended period of undisturbed consolidation time. This period can be the happy flight back to the hive. In any case, when the bee returns to the floral patch, she has a firmly established and well structured memory at her disposal.

(Supported by DFG grant ME 365 / 11 - 3)
REFERENCES


