Temporal dynamics and foraging behaviour in honeybees

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Abstract –*Learning at the feeding site initiates various forms of memory which differ with respect to their temporal dynamics, contents and stability when exposed to successive experiences. Neurobiological analyses indicate that these different forms of memory reside in different parts of the brain: the non-associative memory in the antennal lobes, the associative memory in the mushroom bodies. Single-cell recordings identify neurons which participate in both forms of memory. Behavioural studies were performed to elucidate the question of how these memories guide the choice behaviour of honeybees when collecting food from scattered sites. It is concluded that memory processing in bees is highly adapted to the particular conditions in which the animal has to choose quickly between a large number of potential food sites. A dynamic model is presented which incorporates our knowledge of memory processing in the honeybee.*

Keywords: learning, memory, honeybee, foraging strategy, matching behaviour.

Introduction

The foraging behaviour of nectar-collecting insects has been studied frequently in the past with the aim of understanding not only the ultimate, but also the proximate mechanisms involved in the choice process (Pyke, 1978a; Waddington and Holden, 1979; Waddington, 1985). The currency of fitness is thought to be some- how expressed by the gross or net rate of food gain or energy gain. If the animal is optimizing its fitness, then during its quick flights, we might assume that it continuously carries out rather complicated calculations, which enable it to determine when it should return to the nest, which flower to choose more frequently, which flight path to take, how long to handle each flower, etc. No evidence exists to support the contention that bees, for example, calculate rates between energy invest-

ment and energy gain, time spent in a patch and food gain, probability distributions for reliable or less reliable food sources, travel time between flowers, etc. It therefore appears to us that the models developed (e.g. to conceptualize the optimal diet or the optimal patch choice) are actually human intellectual exercises and have very little, if any, relevance to the processes going on in the insect's brain, which controls the entire job with surprising speed and accuracy.

Another weakness of the optimality models, as far as their proximate explanatory power is concerned, is the fact that the informational component in the foraging process is generally ignored. The nectar-collecting bee does not only collect energy but also, and most importantly, information about the reward conditions of the flowers. At no time is the animal either omniscient or totally ignorant about the food distribution – the two extreme angles from which the optimal foraging theoretician normally works - but has an imperfect and continuously changing informational status. Innate search images and the individual history of learning through experience of potential food sources define, at any given moment, the informational context in which decisions are made.

Here we propose that it is necessary and fruitful to consider learning and memory processes in an attempt to further our understanding of the proximate mechanisms of foraging. It is our suspicion that the internal temporal dynamics of memory processing in the insect brain to a large extent define the rules of decision-making in the foraging process. Thus, an understanding of these processes will help to explain why the foraging behaviour of flower-visiting hymenopterans is so highly adaptable.

Material and Methods

Three experimental paradigms were employed: two using operant learning conditions, and one using classical conditioning:

(1) Operant learning of freely flying bees which are tested in accordance with traditional training experiments (von Frisch, 1965; Menzel, 1967). One individually marked bee is rewarded with sucrose solution from a coloured target in the middle of a round table. On returning to the hive after each reward, the bee is tested for its choice behaviour. Two coloured targets, neither of which contain sucrose reward, are placed at points lying at an equal distance from the place where the bee was previously rewarded. One of these two targets is the same colour as the one used in the training trial. The tests were, therefore, recognition tests in which the bee's choice performance rises according to the strength of the memory of the learned colour target.

(2) Operant learning of freely flying bees which are tested in a multiple choice arrangement. Four feeders are offered which are marked with either the same or different colours. These feeders are arranged horizontally at varying distances (50 cm to 3m). Each feeder produces a constant flow of sucrose solution, but the 4 feeders differ in their rate of flow. In a typical experiment the flow rates were 0.0625 µl/min., 0.125 µl/min., 0.25 µl/min. and 0.5 µl/min. Thus the flow rates have a ratio

of 1:2:4:8. These numbers (1, 2, 4, 8) shall be used in this text when referring to the 4 different feeders. The choice and sampling behaviour of one individually marked bee was monitored continuously with the help of electronic devices which are described in detail in Greggers and Menzel (1993). This experimental arrangement will be called the "matching experiment", because the bee matches its choice of the four feeders to their respective flow rates. Training and testing are, therefore, not separated as in the previous experimental paradigm (1), but are continuous throughout the experiment. The memory of each of the four feeders is expressed by the relative choice of any particular feeder, where the sum of all choices is set to 1.0. The experimental bee usually works for 20 to 30 min. during one foraging bout, and may remain in an experiment for several days, making hundreds of choices during this period.

(3) Classical conditioning of harnessed bees using the proboscis extension reflex (see Menzel 1990 for further details). An indication of the strength of the memory is the probability with which the PER (proboscis extension reflex) occurs when only the CS (olfactory stimulus) is presented. The advantage of working with restrained bees is that the experimenter has full control over the experimental parameters, particularly with respect to the timing of the conditioning trial and the test trial. The conditioning trial consists of the forward pairing of the conditioned stimulus (CS, the odourant carnation) and the unconditioned stimulus (US, sucrose solution). This paradigm also allows us to test the non-associative components of the US, particularly the sensitization caused by the stimulation of the antennae with sucrose solution. The sensitizing effect is expressed in a general arousal, which also enhances the probability with which the proboscis will be extended after presenting the CS.

Results

Memory phases

A life-long memory of a colour signal is already established after 3 operant learning trials (Fig. 1, after Menzel, 1968). A single learning trial will lead to a memory trace which, if the animal is not allowed to learn anything else during this time, fades away a few days after learning. During these early studies it was recognized that the memory improves during the first two hours following a single learning trial.

A careful analysis indicates that the early memory is actually biphasic (Fig. 2a), displaying a high learned performance immediately after the learning trial, a minimum roughly 2-3 min. later, and a rise during the following 10 to 20 min. The same biphasic memory trace is found in the PER conditioning paradigm (Menzel, 1990). It was shown with the help of the PER that the initial high response level during the first 2-3 min. is dominated by the non-associative component of the sensitization caused by the US alone (Menzel et al., 1989; Menzel, 1987; Fig. 2c).

A particularly useful indication of the sensitization is the increase of the proboscis extension response to an odour stimulus before any conditioning to that
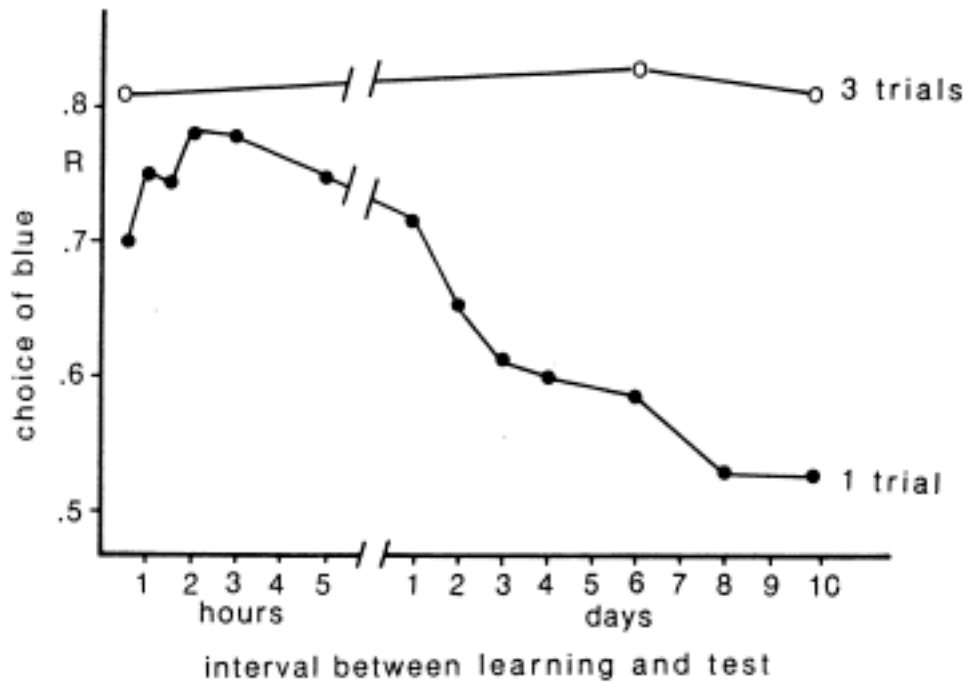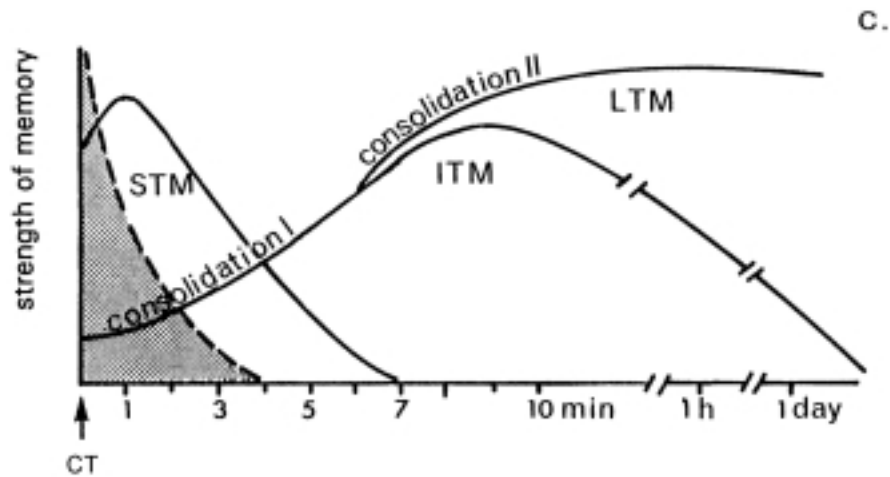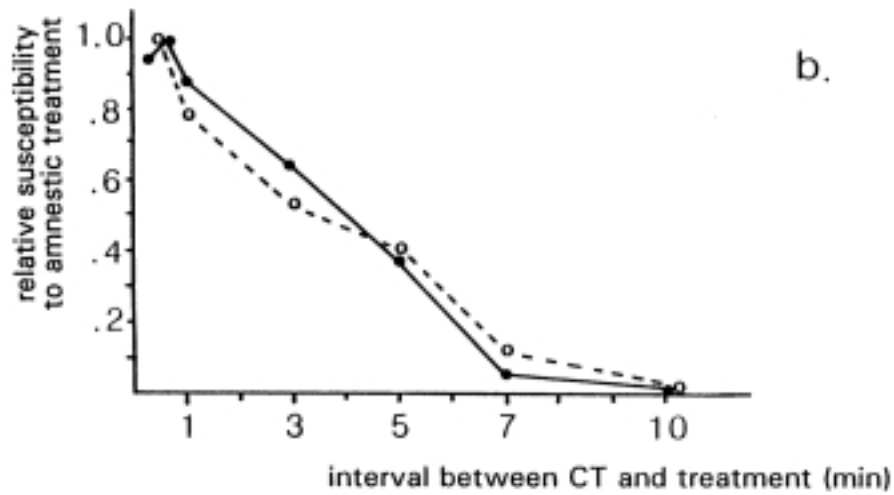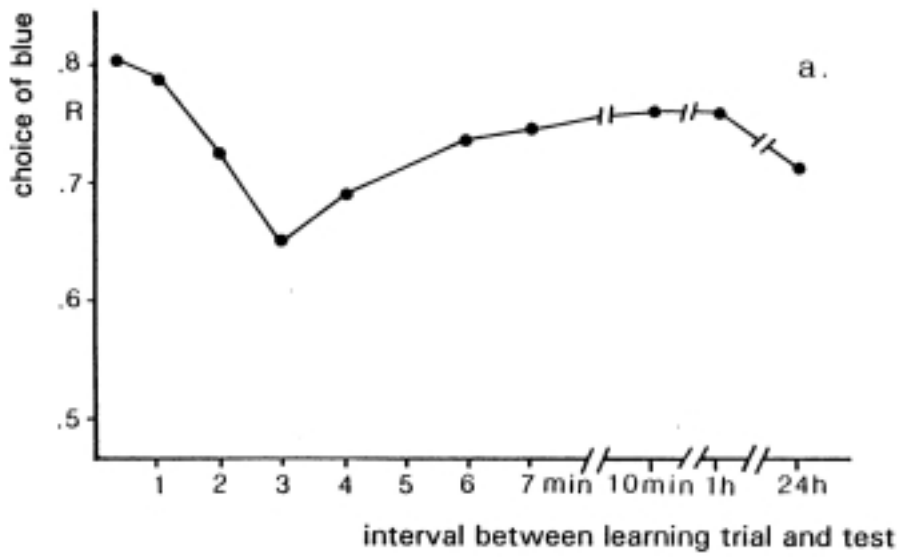
Fig. 1. *Memory of the colour signal of a food source after a single (●) and after 3 learning trials (o). The bees were trained and tested under the operant learning conditions for freely flying bees as described in experimental paradigm 1 in the Methods. Two alternative colours were used (blue and yellow); blue was the training colour (after Menzel, 1968).*

Fig. 2.- a. *The time course of the retention function after a single operant learning trial shows two different phases: the early fast decaying phase and the later rising phase. The proportion of correct choices as tested in the dual test condition with freely flying bees reaches a minimum around 2 – 3 min after the learning trial, and is followed by a consolidation process (after Menzel, 1968).*
b. *Retrograde amnesia initiated by weak electroconvulsive shocks to the brain of the test bees indicates a high susceptibility immediately after the single learning trial and an improving resistance with time. These graphs give the results for the two training conditions, operant learning of freely flying bees and dual-choice test of colour signals (–o–), and PER-conditioning to the odour carnation (--o--) (redrawn from Erber, 1975).*
c. *The model arising from the experiments described in the text assumes three tight, successive memory phases which are connected by two different consolidation processes. (See text). The time course of the non-associative component as determined by the sensitization of the PER immediately after a sucrose stimulation to the antennae is indicated by the stippled area. STM: short-term memory; ITM: inter-mediate-term memory; LTM: long-term memory (after Menzel, 1990, redrawn).*

a.

b.

c.

odour. Hungry bees respond spontaneously to an odour at a level of a few percent up to 30%, depending on the odour used. This spontaneous response level increases drastically following a sensitizing stimulation of either the antennae alone, or both the antennae and the proboscis, with sucrose solution. The response increase declines quickly to a normal level, indicating that the sensitization effect lasts only a few minutes. This means that the memory during the first few minutes is a combination of a non-associative component, which has a general arousal effect and low stimulus specificity, and a slowly rising associative component which has a high stimulus specificity. These different components also manifest themselves in the sensitivity of an early memory trace to an additional learning trial. If the same CS is learned in the second trial, the memory is immediately shifted into its consolidated form and the low performance no longer appears. If, however, a different CS is learned during the second learning trial, and the two learned signals are tested later in a simultaneous test with freely flying bees, the memory trace for the first learned CS is replaced by the second if the learning trials take place in quick succession. If, on the other hand, the second learning occurs more than 3 min. after the first, the first will have already been consolidated, so much so that the second learning trial will only be able to reduce its memory strength partially (Menzel, 1979; Menzel and Sugawa, 1986).

The early form of memory is also extremely susceptible to experimental treatments which initiate a retrograde amnesia. Fig. 2b shows the temporal gradient of the sensitivity to amnestic treatments (such as cooling, weak electroconvulsive shocks or anesthesia) in both operant and classical conditioning (Erber, 1975; Erber et al., 1980; Menzel et al., 1974). The time course follows that of the consolidation after a single learning trial (consolidation I, Fig. 2c). It can, therefore, be concluded that induced retrograde amnesia predominantly affects a memory phase which stores the memory after a single learning trial for a time-span of anything from several hours up to a few days. This interpretation is supported by the fact that learning trials which take place in quick succession (within 1 – 3 min.) establish a memory which is no longer susceptible to retrograde amnesia.

These observations allow the establishment of a model of the memory phases in the honeybee (Fig. 2c). Three temporal phases are closely linked by consolidation processes. Short-term memory (STM) consists of two components: the non-associative and the associative. After a single learning trial the associative component is consolidated into an intermediate form of memory (ITM) which - if not reinforced by additional learning trials – will fade within 1 or a few days. The life-long memory (long-term memory, LTM) is established only by several learning trials and the rate at which these learning trials occur (consolidation II).

The role of specific memories of different food sources during foraging

Under natural conditions bees feed on many flowers before they have filled their crop and return to the hive. Each of the many successive visits to flowers in a patch is a learning trial. If the choice of a flower is combined with even a small reward

of nectar, the corresponding learning trial will be a positive one and will enhance the memory for that particular flower type. If the experience of flower is negative (no reward) the learning may be called negative and reduces the memory of that flower. Experiments have shown repeatedly that positive or excitatory learning trials are much more effective in updating the memory than negative or inhibitory learning trials (review Menzel, 1990).
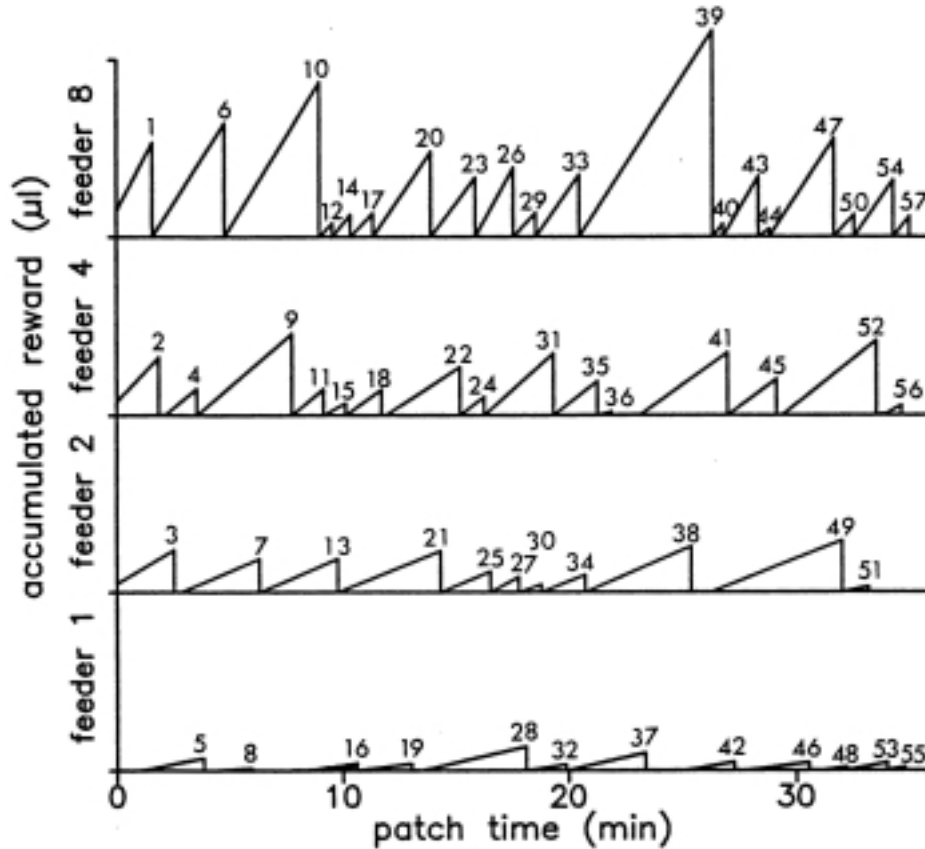

Fig. 3. - *An example of the choice sequence performed by an experimental bee collecting sucrose solution from feeders 1,2,4 and 8 in an operant learning situation for freely flying bees (experimental paradigm 2, see Methods). The record is the full sequence of visits at the four feeders during one foraging bout. The slow rising lines indicate the flow rates of the four feeders and thus plot the amount of accumulated sucrose solution in each feeder. The fast falling lines indicate the sucking of the bee. Consecutive visits are numbered. It is obvious that the bee collects the full amount of accumulated sucrose solution during any visit, regardless of the amount which has accumulated. Furthermore, one can see that the bee visits feeder 8, which has the highest flow rate, most frequently and the other feeders less frequently in a graded fashion (redrawn from Greggers and Menzel, 1993).*

A common situation under natural conditions is that different plant species, or the same plant species flowering at different patches, offer different amounts of nectar. It is obvious that the foraging bee would save time and energy if it concentrated its foraging activities on the most productive flower. Indeed bees are capable of doing this (Heinrich, 1983; Seeley, 1985). The energetic aspects have been of interest to many authors, but the informational aspects have been thus far neglected because little is known about the contribution of learning and memory to foraging under natural conditions. The problems posed by such an analysis are formidable. A knowledge of the individual history of experience over a considerable time span (e.g. days) by following the flight path without any interruptions and measuring the amount of reward at any chosen flower down to quantities of less than the nl range would be necessary.

The experimental set-up we have used to address these questions is described as experimental paradigm 2 in the Methods, and in more detail in Greggers and Menzel (1993). The four feeders produce a constant flow of nectar at differing rates throughout the time the experimental bee is foraging in this small patch. Fig. 3 shows that the bee collects from all four feeders under these conditions and it visits the high reward feeders more frequently than the low reward feeders. The figure also demonstrates that the amount of accumulated sucrose solution is completely depleted during any given visit, and an immediate return to the same feeder will lead to an un-rewarded choice.

The continuous process of flying between feeders, choosing between them, probing and sucking sucrose solution inside the feeder, leaving, flying, and choosing again can be broken down into the smallest behavioral unit depicted in Fig. 4. Each foraging bout which lasts for about 20 - 30 min. consists of about 30 – 50 such behavioral units, and in regard to each of these units we may ask in what way the choice of the next feeder depends on past experiences. If the same feeder is chosen again we call this behaviour "stay flight", and if one of the three alternative feeders is chosen we call it "shift flight".
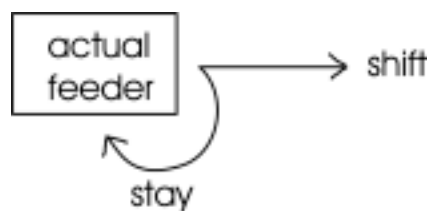

Fig. 4. *The smallest behavioral unit continuously repeated during the foraging process consists of a visit to one of the four feeders, the actual feeder, at which the bee experiences the actual reward (amount of sucrose solution collected). After-wards the bee leaves the actual feeder and departs. If it returns to the same feeder as the actual feeder it will perform a "stay flight", if it chooses any of the 3 other feeders it will perform a "shift flight" (redrawn from Greggers and Menzel, 1993).*
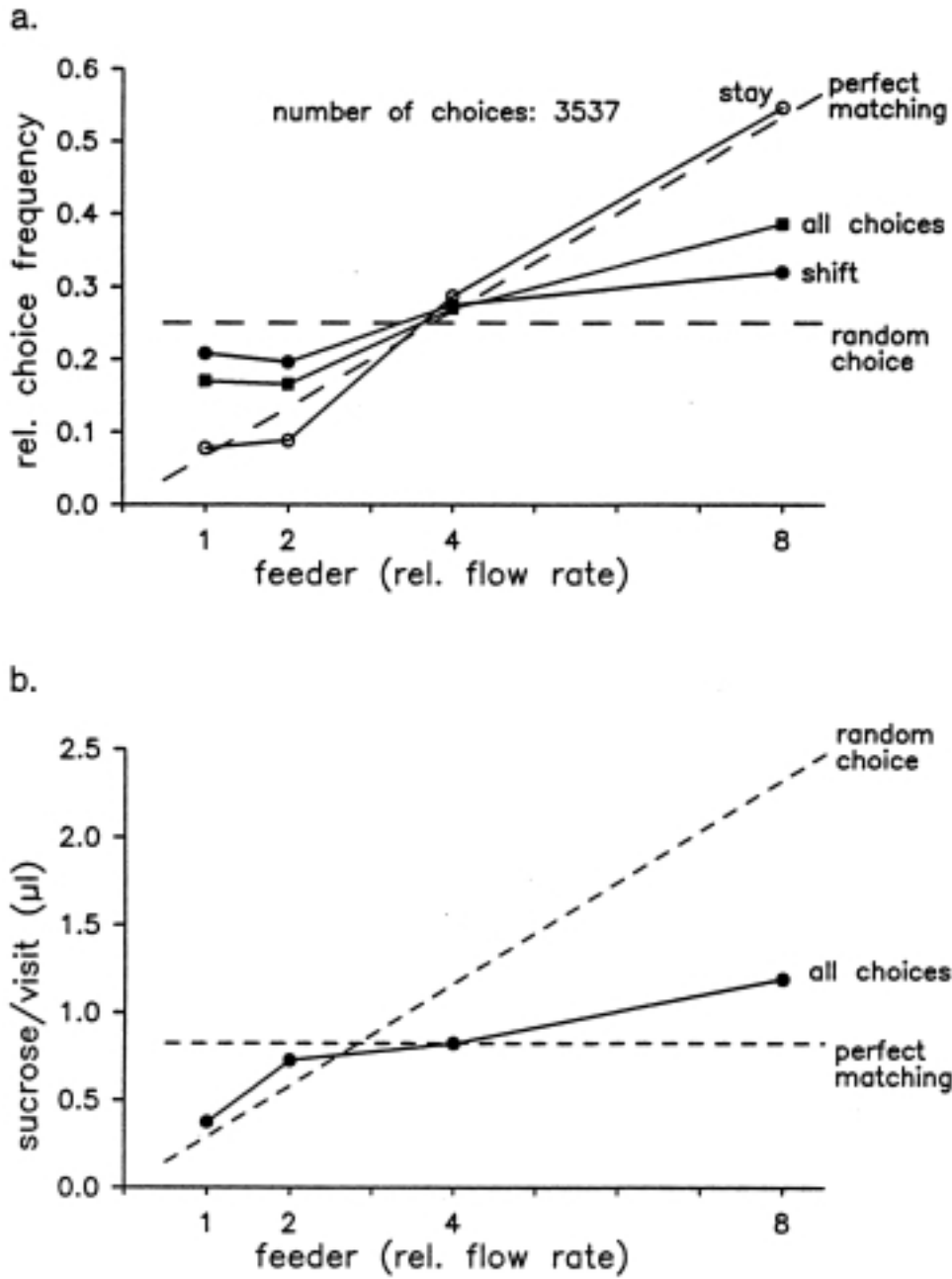
Fig.5. a. *The matching behavior is evaluated for either all choices (curve –) or the two classes of choice flights (stay, ○, and shift,● flights) (see text). **b.** Considering all choices, it is obvious that on average the bee receives a larger amount of reward per visit at feeder 8 because this feeder, which yields most reward, is undermatched (from Greggers and Menzel, 1993).*

Before we analyze the choice behaviour in more detail, we should look at the overall choice proportions of the four feeders. Fig. 5 gives the results of 26 experiments from 130 foraging bouts of 3 different bees with a total of 3,537 choices. It is obvious that the feeder with the highest reward rate is chosen most frequently and the ones with lower reward rates less frequently. Thus the choice behaviour matches the reward rate, at least to some extent. The matching behaviour for all flights (stay and shift flights) normally leads to a higher choice frequency of the low reward feeders when compared with a perfect matching (dotted line in Fig. 5a), and to a lower choice frequency than perfect matching for the highest reward feeder. In consequence, the bees generally collect more volume sucrose solution per visit at the highest reward feeder (No. 8), and less than average reward volume at the two lower reward feeders (Nos. 1 and 2). If the distinction is made between stay flights and shift flights, we find a much better matching between flow rate and choice frequency for the stay flights than for the shift flights.

The latter result suggests that bees might only return to the same feeder if they have just received an amount of reward above a certain threshold, irrespective of which feeder they have just visited. Indeed that would lead, for example, to a more frequent choice of feeder 8 than feeder 4, because the probability of experiencing a supra threshold reward is higher for feeder 8 than for feeder 4. As a result of this behaviour, feeder 8 might also be visited more frequently and at intervals at which no, or very little, sucrose has yet accumulated thus providing, on average, less reward per visit - an observation which was in fact made (Fig. 5b). Such a strategy would predict firstly a step like dependence of stay frequency and amount of actual reward and secondly the same stay frequency/reward amount function for all 4 feeders. Both predictions are incorrect.

As Fig. 6 shows, the frequency of stay flights increases with the amount of reward at the actual feeder in a monotonic fashion. Most importantly, the functions for the four different feeders are not the same. This means that the bee judges a reward of equal amount (e.g. 1 µl) differently, depending on which feeder she received it from. The reward is judged to be unexpectedly high at the low reward feeders 1 and 2, and unexpectedly low at the high reward feeder 8. Another way of describing this effect is to conclude that the bee has learned what to expect from each of the four feeders, and thus the memory of each feeder includes the information about its specific reward quantity, at least in relation to the other feeders.

Temporal dynamics of the memories during foraging

The real time protocol collected by computer on the choice behaviour of the experimental bee allows us to examine the question of whether the two major behavioural categories, stay flight and shift flight, occur with the same, or different temporal dynamics. It appears that the time immediately after termination of the actual visit at one of the feeders initiates a highly dynamic process of memory activation which leads first to a higher probability of stay flights and delayed onset, but rapidly growing probability of shift flights (Fig. 7). Time zero in Fig. 7 is the mo-

ment when the bee departs from the actual feeder and starts flying. Since bees fly at a speed of approx. 2 m/sec. and the feeders are positioned in the experiments reported here at a distance of less than 1 m, the bee would reach the next feeder in less than 1 - 2 sec. Even during a very short stay flight of less than 3 sec. the bee would have the opportunity to cross over at least one alternative feeder. The two different time courses for stay and shift flights are thus not a result of the arrangement of the feeders.
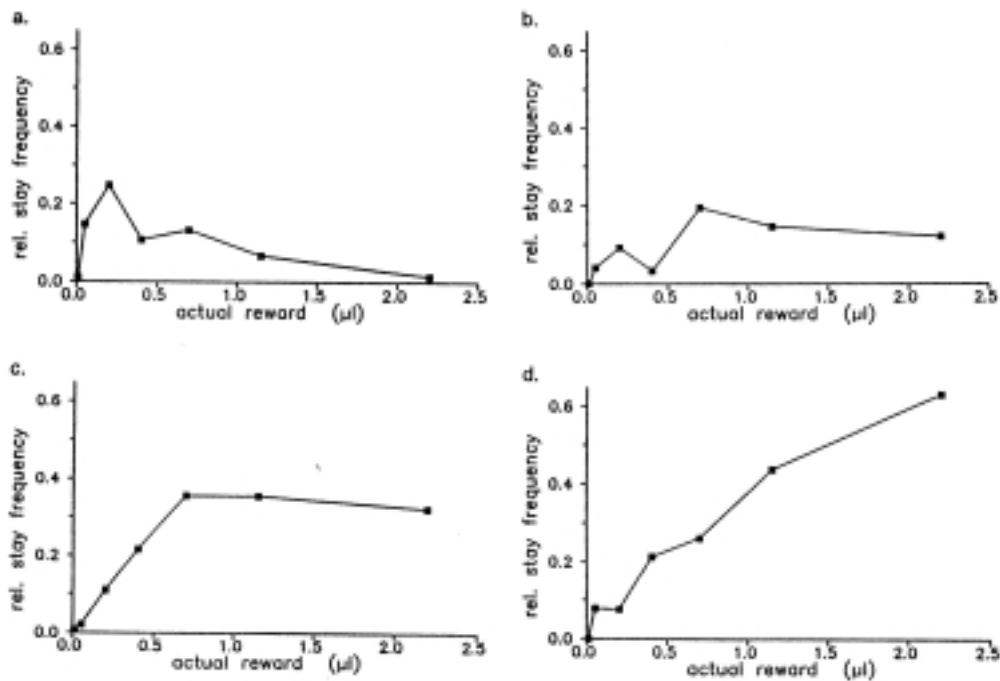

Fig. 6. - *Dependence of the frequency of stay flights at each of the four feeders on the amount of actual reward, a: feeder 1, b: feeder 2, c: feeder 4, d: feeder 8. Each feeder displays a specific function which indicates that the bee doesn't apply the same function to control the stay flight at any given feeder, but has developed a specific memory of the reward quantities for each of the four feeders.*

Since stay flights are progressively initiated by actual rewards exceeding the expected reward, it is tempting to conclude that the high probability of stay flights immediately after leaving the feeder indicates a fast-acting or recent memory which is directed specifically at the feeder which has just been visited. The delayed onset of the shift flights, on the other hand, might indicate the involvement of another kind of memory which refers to previously learned information and may thus be termed

remote memory. As pointed out above, the matching between flow rate in the four feeders and their respective choice frequency is quite different for stay flights and shift flights (Fig. 5a). Therefore, the content of the two memory forms, recent and remote memory, must be different proportion because of the fast stay flights and their high probability for feeder 8.
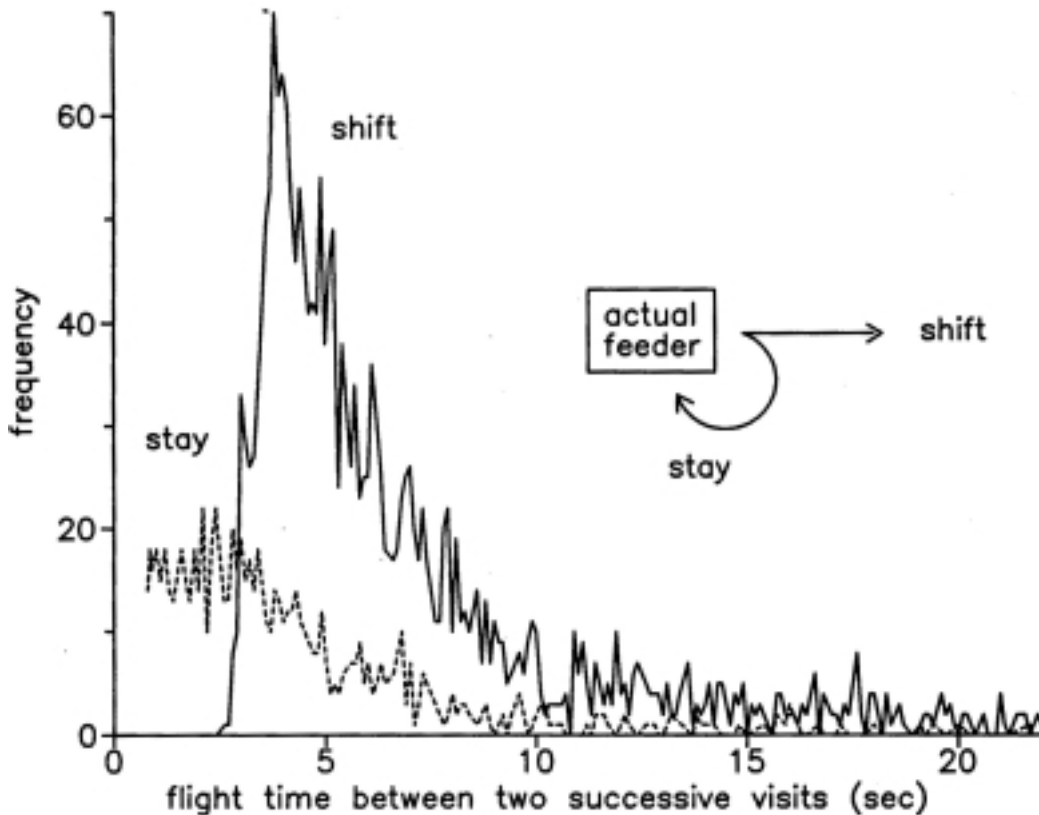

Fig. 7. *The time course of the frequency of stay flights and shift flights during the period between two successive visits. Stay flights occur much faster than shift flights, which appear after a delay of a couple of seconds (see text). (from Greggers and Menzel, 1993).*

It is thus to be expected that the overall choice frequency (stay and shift flights) should be highly dynamic and change considerably during the period immediately following the last visit to a feeder.

This is indeed the case (Fig. 8). The dynamic interaction of contributing memories results in time courses of choice frequencies for each of the four feeders which differ drastically. The highest reward feeder 8 is first chosen at a very high

proportions because of the fast stay flights and their high probability for feeder 8. The choice frequency drops within 5 seconds to a stable level, which now lies below the choice frequency of feeder 4. Feeder 4 is chosen much less frequently during the first 5 sec. but becomes most attractive at longer intervals. The low reward feeders 1 and 2 go through an optimum of choice frequency around 5 sec. after the last visit, just at the time when the choice frequency for feeders 4 and 8 cross.
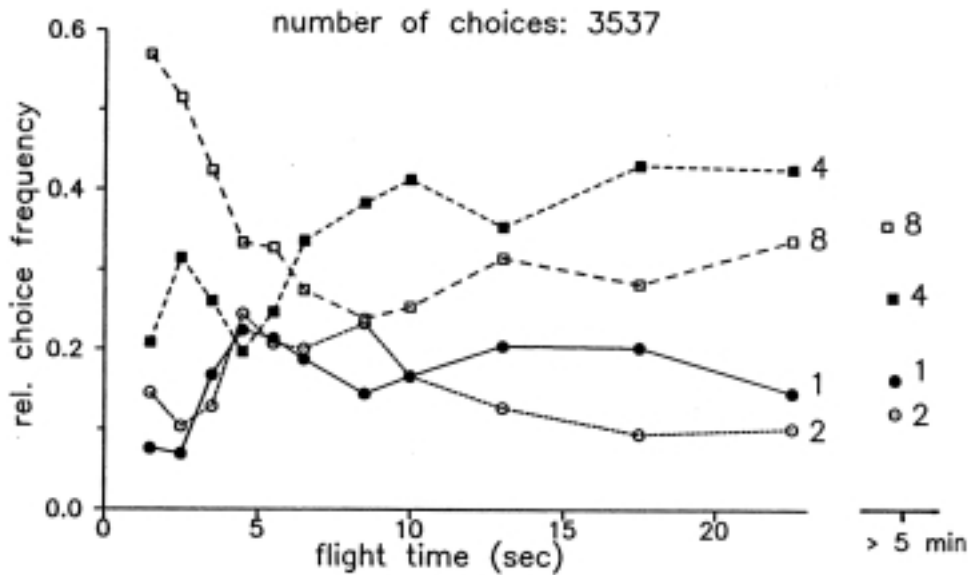

Fig. 8. *The average time courses of all choices to the four feeders during two successive visits. The unconnected data points at the right side indicate the choice frequencies of the four feeders during the first few minutes after return from the hive. The relative choice frequency (ordinate) expresses the choice frequency for each of the four feeders relative to the sum of all choices at that particular time (redrawn from Greggers and Menzel, 1993).*

Fig. 8 also includes the data points for choice frequencies during the first minute after the test bees have returned from the hive. These first choices should be dominated by a long-term memory. The results show that in the long-term memory, feeder 8 has lost its strong attraction and ranks very close to feeder 4. Also, the choice frequencies of the two low reward feeders are very close, although statistically significantly lower than those of the two high reward feeders. The consolidation into a long-term memory has obviously rearranged the memories of the reward quality of the four feeders. Now the low reward feeders are the targets of more choices and are thus upgraded in value, whereas the two high reward feeders are downgraded. This finding may be interpreted as an indication of a comparison of

information in favor of a memory for the average reward quality of the whole patch. At least the dynamics in the choice frequencies indicate the processing of previously stored information after the actual learning.

Conclusion

A model of memory dynamics during foraging in honeybees

A foraging bee arriving at a potential food site relies on innate and previously learned information to guide its choice behaviour. Both these sources of information act together and are also likely to interact during the internal processing of previously learned information. Our studies have clearly shown that the memory ex- pressed in this situation is not just what it was when the animal last left the patch. Rather, patch-specific and target- specific information is combined and activated by the signals provided by the whole patch and the individual targets. The retrieval of the patch-specific and target-specific long-term memories leads to assumptions about the whole patch and the individual targets. Our model assumes as a central thesis that the experienced reward quantity is compared to the expected one. The deviation between experienced and expected reward is a major factor in both updating the memory (learning) and activating a recent or remote memory. The first aspect - learning - has not been considered further in this contribution and is analyzed in a separate paper (Greggers and Menzel, 1993). Here we have shown that an actual reward higher than the one expected for the specific target activates a recent memory and leads to a high probability of re-choosing the same target. An experienced reward lower than the expected one appears to activate a remote memory, which consists of processed target-specific and patch-specific memories. The distinction between these two forms of memory is supported by the discovery of different time courses of stay flights and shift flights.

These temporal dynamics provide us with some hints as to how the three forms of memory identified in the multi-trial matching experiment may relate to the three memories described above, regarding the one-trial conditioning experiments. The absolute time courses differ greatly. In the case of the one-trial conditioning experiments the STM and ITM range from several min. to many hours. In the case of the multi-trial matching experiment the recent and remote memories last for seconds or minutes (compare Fig. 2c with Fig. 7). However, it has been known for a long time (Menzel 1968, Erber 1975) that the consolidating process leading to a stable LTM is greatly facilitated by promptly repeated learning trials. Furthermore, Menzel and Sugawa (1986) have shown that a second learning trial following quickly a first one does indeed shift the content of the STM into LTM. It is tempting to conclude, therefore, that the consolidation process is speeded up by multiple and highly frequent learning trials, and that the long- lasting STM and ITM after a single learning trial correspond to the recent and remote memory phases as seen in the multi-trial matching experiment.

If this interpretation is correct, we may combine observations on the corresponding memory phases and characterize them as follows:

The recent memory (corresponding to the single trial STM) (1) has a high non- associative component, which lasts for even shorter periods than the associative component and is highly dependent on the US strength, whereas the associative component is only mildly dependent on the US strength; (2) it is less specific to target signals; (3) is highly sensitive to interference (such as external disturbance or negative experience); (4) it has a fast decay constant during which a consolidation-I process leads to the ITM.

The remote memory (corresponding to the single-trial ITM) (1) has a low non- associative component; (2) is highly specific regarding the target signals; (3) is more resistant to interference; (4) has a slower decay constant during which a consolidation-II process leads to a stable LTM.

The model of the foraging process developed on the basis of the memory phases is very different from the models so far discussed in the literature (Pyke, 1978b; Schmid-Hempel, 1985, 1986 and with the exception of Heinrich, 1984). Our model contains no random walk components, no assumptions about the direction of the flight path in dependence of the amount of reward, no calculations of ratios of any kind (see Introduction). Rather, the model is based on the time- and event-dependent internal processing of different and successive memory phases which guide the choice behaviour of the animal in a world of memory-tagged objects.

More experiments are reported by Greggers and Menzel, 1993), and the model is further developed with respect to the continuous learning process during foraging.

References

Erber, J. (1975). The dynamics of learning in the honeybee *(Apis mellifera carnica)*.I. The time dependence of the choice reaction. *J. Comp. Physiol., 99:*231-242.

Erber, J., T. Masuhr, and R. Menzel. (1980). Localization of short-term memory in the brain of the bee, *Apis mellifera. Physiol. Entomol., 5:*343-358.

Frisch, K. von (1965). *Tanzsprache und Orientierung der Bienen,*Springer, Heidelberg, 578 pp.

Greggers, U. and R. Menzel. (1993). Memory dynamics and foraging strategies of honeybees. *Behav. Ecol. Sociobiol.* 32, 17-29

Heinrich, B. (1983). Do bumblebees forage optimally, and does it matter? *Am. Zoologist, 23:*273-281.

Menzel, R. (1967). Untersuchungen zum Erlernen von Spektralfarben durch die Honigbiene *(Apis mellifica). Z. vergl. Physiol., 56:*22-62.

Menzel, R. (1968). Das Gedächtnis der Honigbiene für Spektralfarben. I. Kurzzeitiges und langzeitiges Behalten. Z. *vergl. Physiol., 60:*82-102.

Menzel, R. (1979). Behavioral access to short-term memory in bees. *Nature, 281:*368-369.

Menzel, R. (1987). Memory traces in honeybees. In: *Neurobiology and Behavior of Honeybees* (R. Menzel and A. Mercer, Eds.). Springer, Berlin, pp. 310-325.

Menzel, R. (1990). Learning, memory, and "cognition" in honey bees. In: *Neurobiology of Comparative Cognition* (R.P. Kesner and D.S. Olten, Eds.). Erlbaum Inc., Hillsdale, N.J., pp. 237-292.

Menzel, R., J. Erber, and T. Masuhr. (1974). Learning and memory in the honeybee. In: *Experimental Analysis of Insect Behaviour* (L. Barton-Browne, Ed.). Springer, Berlin, pp. 195-217.

Menzel, R., M. Hammer, and M. Sugawa. (1989). Non-associative components of conditioning in honeybees. In: *Neural Mechanisms of Behavior* (J. Erber, R. Menzel, H.J. Pflüger and D. Todt, Eds.). Georg Thieme Verlag, Stuttgart – New York, p. 221.

Menzel, R. and M. Sugawa. (1986). Time course of short-term memory depends on associative events. *Naturwissenschaften, 73:* 564-565.

Pyke, G.H. (1978a). Optimal foraging in bumblebees and coevolution with their plants. *Oecologia, 36:* 281-293.

Pyke, G.H. (1978b) Optimal foraging: movement patterns of bumblebees between inflorescences. *Theor. Pop. Biol., 13:* 72-98.

Seeley, T.D. (1985). *Honeybee ecology. A study of adaptation in social life,* Princeton Univ. Press, Princeton, 202 pp.

Waddington, K.D. (1985). Cost-intake information used in foraging. *J. Insect Physiol., 31:* 891-889.

Waddington, K.D. and L.R. Holden. (1979). Optimal foraging: on flower selection by bees. *Am. Nat., 114:* 179-196.