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# Sensori-motor learning and its relevance for task specialization in bumble bees

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**Abstract** Individual bees often restrict their visits to only a few species out of the multitude of available plants. This flower constancy is likely caused by limitations of memory for motor patterns, sensory stimuli, or reward levels. Here we test the implications of sensori-motor learning and memory for flower constancy. Artificial "flowers" with two distinct "morphologies" were used, so that in each flower type, a different motor pattern was needed to reach the nectar. As in natural flowers, these morphological types were associated with sensory signals (blue and yellow color stimuli). Bees which learned only a single task were more efficient in several ways than those which had learned two: they made fewer errors, had shorter flower handling times, took shorter times to correct errors, and transitions between flowers were initially more rapid. For bees which had learned two tasks, performance depended strongly on the training schedule: if each task was learned with blocked trials, the memory for the second appeared to interfere with that for the first. Interference affected only the association between flower signal and motor pattern, not the motor pattern itself. This was not the case if bees were trained for both tasks with alternating trials. In that case, bees rapidly learned both tasks, albeit with worse saturation levels than bees which had learned only one. Bees transferred the experience gained on one task to a second task: their initial performance on the second task was better than their initial performance on the first. On the other hand, performance on the second task in the *saturation* level (in which bees no longer improve their efficiency) was worse than on the first task (negative transfer). In the saturation phase, performance did not directly depend on switch frequency, but on whether the bee had one or two options in memory. Thus, while bees would become proficient at two tasks more quickly if their acquisition phase included switches, such switches had no measurable effect in the saturation phase. The implications of these findings for foraging are discussed using modern learning theory.

**Key words** *Bombus impatiens* · Flower constancy · Memory · Motor learning · Specialization

## Introduction

In about 350 BC, Aristotle observed that "during each flight the bee does not settle upon flowers of different kinds, but flies, as it were, from violet to violet, and touches no other till it returns to the hive" (cited in Christy 1884). This form of temporary specialization, now termed flower constancy, is defined as follows: an individual insect is constant if it visits only a restricted number of flower species, even if other species are available and equally rewarding, and if the insect has no innate or imprinted predisposition to visit only flowers of a restricted systematic group. The latter must be confirmed by the observation that other individuals of the same insect species visit other plant species within the same array (Waser 1986).

Whilst some scientists conjectured that flower constancy is adaptive in maximizing foraging efficiency, it is obvious that, given two flower species with equal abundance and equal rewards, it is not advantageous to visit only one species and bypass all flowers of the other (Waser 1986). Most researchers now agree that memory limitations cause insects to specialize temporarily on a single or few flower species out of those available (Waddington 1983; Lewis 1986; Waser 1986; Laverty 1994a; Chittka et al. 1997). However, there is no

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agreement on the question of what specific limitations of learning and memory are responsible. For example, is constancy caused by limitations in sensory learning, i.e., can bees only memorize the color, pattern, odor, and size of the flowers of only a single species? Or are there limitations in motor learning, i.e. can bees only learn how to handle flowers of a single structure?

The problems become even more complex when one takes into account the potential limits of storage capacity and retrieval efficiency: can bees only *store* the signals (and/or handling patterns) of flowers of one flower species? In that case, there are two possible consequences, both of which will favor constancy: either, the learning of a flower is an imprinting-like process which results in a fixed preference and cannot be altered through the life of an individual (proposed, without evidence, by Faegri and van der Pijl 1979); or, the memory for the flower species learned first will be erased when a bee familiarizes itself with a second one, as was claimed for *Pieris* butterflies (Lewis 1986). Alternatively, there might be no strong limitations on *storage capacity*, i.e., bees might well be able to memorize flowers of several species (which indeed they can: Kugler 1943; Menzel et al. 1993), but incur costs (such as increased decision times, error rates and handling times) when the memories for different flower types are *retrieved* alternately, rather than repetitively (Heinrich 1976; Laverty 1994a; Schmidt 1991; Chittka et al. 1997).

Finally, the distinction of short-term and long-term memory is important: Although Lewis (1986) found that the long-term memory of butterflies for one flower species will be erased when a second species is learned, Menzel (1979) found that this is not so in honey bees. Their long-term memory easily holds the properties of the flowers of several species, but Menzel found a direct interference effect in short-term memory: if honey bees are given two subsequent learning trials with two different colors, the memory trace for the first color can be effectively erased if the second trial follows immediately after the first trial.

Here, we use artificial flowers with distinct morphologies to assess the relevance of limitations of *motor* learning and memory, and associations of color signals with motor patterns (*sensori-motor* learning), on flower constancy. Motor learning is important in foraging from flowers, because the ways in which bees have to move their bodies to get to the floral reward differs grossly between plant species: while some flowers present the nectar in open cups, and thus provide easy access to the nectar, many have extremely intricate morphologies that require complex handling skills (Faegri and van der Pijl 1979; Laverty 1994b), and there are even left-right asymmetries (*enantiomorphisms*) in floral morphologies (Fenster 1995). However, the relevance of motor learning for flower constancy is poorly understood.

A number of workers, dating back to Darwin (1876) have suspected limitations of motor learning as a likely cause of flower constancy (e.g., Heinrich 1976; Waddington 1983; Waser 1986), but the evidence is controversial: bumble bees (Kugler 1943) and honey bees (Menzel et al. 1993) can certainly store more than one odor and color in their memory, but their memory capacity for motor tasks is unknown. Woodward and Laverty (1992) and Laverty (1994a) found that bumble bees have slightly longer handling times immediately after switching between some species, but no such costs were observed in several other pairs of species. Thus, bumble bees certainly do not start from scratch at learning to handle a flower morphology after every switch to another species. L. Chittka (unpublished work) reanalyzed data from Chittka et al. (1997) and found no evidence for increased handling times after transitions between species. However, in these studies, either the experience of the individual insects prior and during the tests, or the reward levels during the tests, or the comparability of tasks were not controlled. Thus, these experiments do not allow a conclusive answer to the question of which particular memory limitation might be responsible for temporary task specializations in foraging insects.

Here, we test bees which are entirely naive as foragers at the onset of the experiment. We employ a rigorously controlled setup, using electronically monitored artificial flowers with distinct morphologies. We ask the following specific questions:

1. Does learning one task influence the speed of learning a second?
2. Does learning the second task interfere with the memory for the first?
3. Is there a decrease in performance if a bee has to cope with more than a single task?
4. If so, which parameters of performance are affected: handling times, error scores, the speed with which tasks are learned and errors are corrected, or transitions between flowers?
5. What is the better schedule for storing two tasks in memory: several consecutive trials on each task, or alternating tasks after each trial?
6. Once tasks are stored in memory, does it matter if they are retrieved in an alternating fashion, or whether bees stick to each task for several consecutive trials?
7. Does performance decline overnight?

## Methods

### The bees

Bumble bee colonies (*Bombus impatiens*) were obtained from Koppert Biological Systems Mich., USA). They were kept in a nest box which was connected to a flight arena of 60 cm × 40 cm (28 cm height) by means of a transparent plastic pipe. Manual shutters in the pipe allowed us to control which bees entered the arena. A large number of bees were individually marked with Opalith-Plättchen and only marked individuals were tested. Pollen was fed directly into the nest. Between experiments, bees could forage freely from a clear styrene feeder (a Petri dish with holes drilled into the top), which contained 50% (volume/volume) sucrose solution, and which was located in the center of the flight arena. The only foraging experience the bees had prior to training was extracting sucrose solution from this openly accessible feeder. Thus, they were naive not just with respect to the experimental task, but with respect to foraging from any structure that might resemble a flower.

## The flowers

In the flight arena, bees had access to four artificial "flowers" which were blocks of polyethylene with channels milled into them. The entrances to the flowers were in one of the walls of the flight arena. The entrances were arranged side by side, with distances of 10 cm between them. The entrance hole was square (6 mm × 6 mm) and each hole was surrounded by a yellow or blue colored square (3 cm × 3 cm). The inside of each flower had the shape of a T-maze (Fig. 1). The entrance tunnel measured 14 mm, and both arms were 17 mm in length; all tunnels had the same width as the entrance of the flowers. The rationale for this simple flower design was that left and right turns constitute two tasks that are different but exactly equal in difficulty. In all experiments to be described, the reward was offered in the right arm of the flower when the entrance bore a blue mark, and in the left arm when the entrance was yellow.

What is the similarity between T-mazes and natural flowers? Flowers have sensory signals (colors, odors) which are used by the animals not only as learned predictors of nectar reward, but also as predictors of the particular motor pattern needed to extract the nectar. In natural flowers and in the T-mazes, the bees have to learn to move their bodies in a particular way to get access to the reward, and these learned movements must be guided by sensory stimuli that define a flower type, or in our case, a maze type.

The entrance and each arm of the mazes were controlled by infrared light barriers that signaled a computer when the bee broke the beam at each of three locations (Fig. 1), so that behavior could be evaluated on-line. Under each maze arm was a sliding plexiglas rail with a linear series of nectar wells, 1.5 mm in diameter and 3 mm deep, drilled into the plexiglas. If a well was emptied, the rail was advanced so that the next reward was made available. In this way, the entire floor of both arms of the maze was replaced, so that if bees should leave odor marks on the floor, these could not be used during subsequent visits. Each plexiglas rail had 25 wells, and every well contained 5 µl of 50% sucrose solution, so encouraging bees to visit several flowers (typically 20–30) before returning to the nest with a full stomach (one such round-trip is a *foraging bout*).

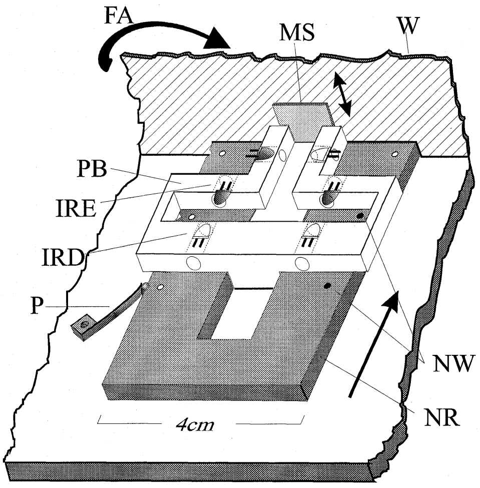

**Fig. 1** Schematic drawing of one of the four "flowers", with the roof removed. During experiments, each "flower" is covered with a red translucent plastic sheet. [*FA* flight arena, (behind the wall), *IRE* infrared emitters, *IRD* infrared detectors, *MS* manual shutter to control access to the maze (the *double-headed arrow* shows the directions of movement), *NR* - "nectar" rail, sliding under the arms of the maze, so that the rail forms the floor of the maze in the arms, *NW* nectar wells (*black* full, *white* empty), *PB* polyethylene block which constitutes the walls and the central (*white*) part of the maze floor, *P* spring-loaded indexing pawl that engages regularly spaced notches on the nectar rail, allowing fresh nectar wells to be quickly and precisely clicked into position between visits, *W* wall of flight arena (which bears the color marks at the entrance holes of the mazes). The nectar rail slides under the floor of the flight arena. The *single-headed arrow* marks the direction in which the nectar rail is advanced

## Pretraining

Bees were trained and tested individually. For each bee, the whole procedure comprised 600–800 trials (flower visits), of which the first 400 were completed on the first day, and the remaining trials on the subsequent day. During this procedure, no other bees were allowed in the flight arena, and the experimental bee was never fed at any food sources other than the experimental flowers, except possibly inside the nest. A single bee was selected from those feeding from the clear plexiglas feeder; this was done by observing the feeder for some time, and then picking a bee which arrived at that feeder with a particularly high frequency. No other bees were then allowed in the arena, and training could begin.

Naive bees never explored the flowers on their own; thus, a pretraining procedure was necessary to start visitation. The feeder was moved in a few steps from its central location of the flight arena to the entrance of a fifth flower, the pretraining flower. A move was performed each time the bee had gone to the nest, so that, on returning, the bee would find that feeder in a novel location. Finally, when the bee had once fed at the feeder location directly at the entrance of the pretraining flower, the feeder was removed. Before the bee returned from the nest, a flexible tube was inserted through the back wall of the pretraining flower, so that it extended all the way through the entrance tunnel and to the entrance of the flower. This tubing was connected to a container with 50% sucrose solution, which was adjusted in height so that the bee could easily drink from the end of the tube. When the bee returned, it would not find the familiar feeder, but would search the area and eventually find the tube. Then, as she sucked, the tube was slowly pulled back through the entrance tunnel, until its end was all the way at the back wall. The bee would follow the retracting tube. She was then allowed to suck until she entirely filled her honey stomach. Then she went home, and when she came back from unloading her crop, the tube had been inserted from one of the sides of the maze, so that its end extended to the center of the maze (where the bee had previously sucked from it). The side from which the tube was inserted depended on the training color: if the bee was to be trained to blue, the tube was inserted from the right arm of the maze, and from the left end if the bee was to be trained to yellow. Again, once the bee had found the tube, it was retracted slowly until the tube (and the bee) had reached the end of the maze's arm. There, the bee was again rewarded *ad lib*. This final step, in the pretraining procedure (i.e., training the bee from the central part of the maze to one of its arms) is called a *pretraining trial*.

## Training and test schedules

Three groups of bees were trained, one on only one task, the others on both tasks, but with different training schedules. The insides of the flowers were cleaned with alcohol after every second foraging bout. To prevent bees from simply using the position (and not the color) of a flower entrance to identify the correct direction, the blue entrance marks were exchanged for yellow ones (and vice versa) after every other foraging bout. The rails containing the rewards were exchanged accordingly, so that blue flowers would again contain the reward on the right side, and yellow ones would offer them on the left.

During the tests, bees could choose freely which flower to exploit next, with two restrictions: (1) they could not directly return to the flower just visited; and (2) when switching between flower types was enforced, both flowers of the previously visited type are made inaccessible. Access to the flowers was controlled by manual shutters which slid into a 1-mm crevice between the color cardboard and the actual entrance tunnel of the flowers. A reward was offered at each visit; even when bees initially turned into the wrong arm of the maze, they were allowed to correct this error and feed in the opposite arm.

### Group 1 (six bees)

After a single pretraining trial on their respective task (either to associate a blue entrance with a right turn, or a yellow entrance with a right turn) bees were given 600 trials on only a single task. Three of the bees were trained to blue flowers and the other three to yellow flowers. These tests were necessary to examine how fast bees learned a single task, and to see whether this rate would be comparable to those in natural flowers, as established by Laverty (1994b). Moreover, this group serves as a control for the two following groups, which were both trained on two tasks, so that we could test if there is at all a decrease in performance if bees have to cope with more than a single task.

### Group 2 (seven bees)

Bees of this group had to learn two tasks, both to associate blue with right turns, and yellow with left turns. Four of the bees were trained to blue flowers first, and three were first trained on yellow flowers. All bees received 600 trials. Training was done by means of a blocked schedule: bees were first given a pretraining trial on the first task, then 100 trials on the first task (e.g., blue-right). After this followed a pretraining trial on the second task, and subsequently 100 trials on that second task (e.g., yellow-left). Finally, the bees were given 400 trials during which they were forced to switch between tasks after each trial. The first trial in this final series was on the task that bees had learned first. These tests were run to determine if learning the second task would interfere with the memory for the first, or, if learning the first task would facilitate learning of the second. We also wished to know if performance would decay, once both tasks were stored in memory, or once bees were forced to switch between tasks.

### Group 3 (five bees)

Bees of this group were also trained on both tasks, but with a different schedule. As opposed to bees of group 2, these bees were forced to alternate between tasks after each individual trial; 300 trials of each task were given. Pretraining in these bees was done by administration of one pretraining trial on the first task, and immediately on the next foraging bout, a pretraining trial on the second. The rationale of this experiment was to test if bees could learn two different tasks if they were forced to switch continuously between them. The two different training schedules for groups 2 and 3 were chosen to see if a blocked or mixed schedule is more efficient for learning two tasks. During 400 trials, bees of groups 2 and 3 had to cope with precisely the same task, i.e., to switch continuously, between "blue-right" and "yellow-left" respectively. Both groups are comparable in that they have received equal numbers of trials previous to these 400 (i.e., 100 trials on blue, and another 100 on yellow). They differ only in the sequence of the first 200 trials. What is the better schedule for storing both tasks in memory?

After 600 trials were completed in the fashion described above, bees of group 3 were given between 100 and 200 trials during which they were forced to switch after runs on each tasks with a random length between one and ten trials. This was done to make sure that what bees had learned was not simply that a left turn always follows a right turn and vice versa, but rather that blue was associated with right turns, and yellow with left. In addition, we wanted to ask if the bees performance in saturation (when they were already familiar with both tasks) could be improved by decreasing transition frequencies between tasks.

## Data evaluation and statistics

### *Error scores*

Two types of errors were analyzed. *Aborted visits* were visits in which a bee entered only the entrance tunnel of the flower, without turning into one of the side arms. These visits were unrewarded. *Direction errors* occurred when a bee initially turned into the wrong arm before feeding. Error scores were determined as follows. For each bee, the 600 ordered visits were categorized into 60 bins of 10 consecutive visits. The number of errors of each type within each bin were counted. Next, we tested whether bees within a group were statistically homogeneous with respect to the number of errors in the 60 bins for each bee, using $n \times 60$ contingency tables. Learning curves were established by plotting the percentage of errors in each bin of 10 consecutive visits, as a function of the midpoints of the bins (Fig. 2). Chi-square $2 \times 2$ tables were used to test if rates of correct visits in each bin were distinguishable from chance. Finally, to see if the different training schedules affected performance, we performed between-group comparisons, applying chi-squared goodness-of-fit tests to the pooled error scores of each group.

### *Handling times*

Handling times are defined here as the times taken by the bees to navigate the mazes, excluding the times taken to imbibe the nectar (the times a light barrier in the nectar-containing arm of the maze was continuously broken during a single visit). We fitted first-order exponential decay functions to the handling time data, so modeling the learning curves, using the non-linear least-square fitting procedure provided by Microcal Origin 4.0. Such functions can be described by:

$$y = y_0 + Ae^{-x/t} \tag{1}$$

where $y_0$ is the $Y$ offset, the asymptotic value on the $Y$ scale (handling times in our case) for large $X$ values; $t$ is the decay constant (it is small when the curve approaches $y_0$ rapidly, and large when the slope is shallow); $t$ is thus a measure of the learning speed. $A$ is the amplitude; it specifies the height of the curve above $y_0$. The sum of $y_0$ and $A$ marks the ordinate value of the curve at $x_0$; it is thus a measure of the handling time at the beginning of training. To give an indication of how quickly a high level of performance is reached, we also give the trial number at which the fitted exponential decay function has fallen four-fifths of the way from its initial value to its saturation level (80% criterion). Handling times are given here only for error-free visits; those visits which began with a turn into the wrong arm of a flower (*direction errors*) are analyzed separately.

### *Correcting errors*

Ideally, a bee should learn to avoid errors, so that correcting an incorrect decision becomes unnecessary. However, under some conditions bees have to cope with error levels above zero for the entire duration of the experiment (see results). Thus, we also tested whether bees improve their speed at correcting direction errors, again by fitting exponential decay functions to the times taken to correct errors, as a function of the number of trials. We also tested whether the times taken to correct errors depended on the number of tasks learned.

### *Between-flower times*

Field observations showed that transitions between flowers of different species take longer times than flights between conspecific species, independently of distance (Chittka et al. 1997). To test for such an effect here, we evaluated the times taken to travel between flowers, and examined whether they depended on the number of tasks that bees were trained on. To this end we compared the

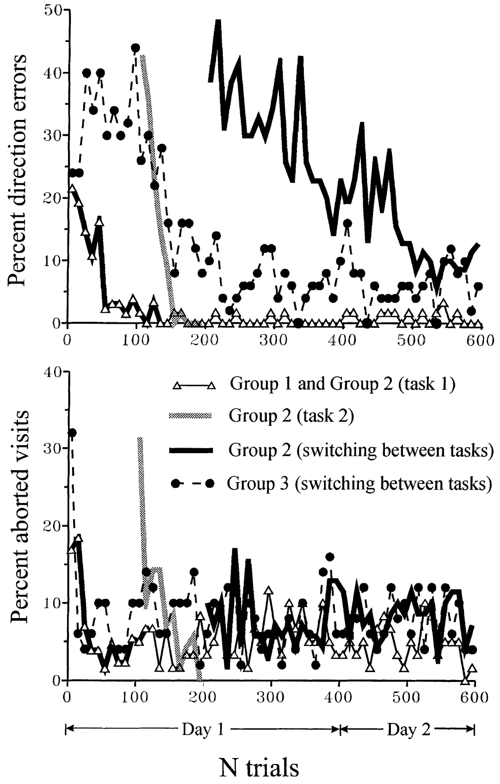

**Fig. 2** Error scores for bees of groups 1–3. Each point categorizes 10 subsequent visits from each group. The *top* part shows *direction errors* (turns into the wrong arm of a maze); the *bottom* part shows *aborted visits* (where bees entered the entrance of the maze, but left it without entering any of its arms). Since group 2 is given the same treatment as group 1 during the first 100 trials, a joint curve for both groups is shown for trials 1–100 (*triangular symbols*, *bold* segment of curve). Data produced by group 2 (or to which this group contributed, see above) are denoted with bold curves. For direction errors, note that (1) bees coping with two tasks (groups 2 and 3) performed worse than those trained to only one task throughout the entire experiment, and (2) there is a dramatic difference between groups 2 and 3 during trials 201–600, even though both groups had received equal numbers of trials on both task during trials 1–200. Thus, the poor performance of group 2 (*black bold line without symbols*) in the switching phase is entirely a result of its blocked training schedule. Rates in aborted visits were more similar between groups, but bees trained on only one task (*triangular symbols*) generally outperformed all bees trained on both tasks

performance of groups 1 and 3. Times taken to travel to the nest and back are not included in this analysis.

## Results

### Error scores

#### *Tests for homogeneity*

The error scores of group 1 were homogeneous between individuals, both for *aborted visits* (where bees only entered a flower and left without choosing a direction; $\chi^2 = 321.4$, $df = 295$, $P = 0.139$ and *direction errors* (where bees chose the arm of the maze; $\chi^2 = 318.7$, $df = 295$, $P = 0.164$). The bees of group 1 and 2 were given the same treatment during the first 100 trials; therefore, we also tested all 13 bees for homogeneity. There was no significant difference between bees ($\chi^2 = 124.9$, $df = 108$, $P = 0.126$). With the exception of one set of data, the error scores for all other groups of bees were also homogeneous (direction errors: $\chi^2 = 351.1$, $df = 354$, $P = 0.533$ for group 2; $\chi^2 = 244.8$, $df = 236$, $P = 0.33$ for group 3; *aborted visits* for group 3: $\chi^2 = 255.3$, $df = 236$, $P = 0.188$). The only set of data that showed significant interindividual differences were the aborted visits for group 2 ($\chi^2 = 427.3$, $df = 354$, $P = 0.005$). Thus, we examined this data set in more detail to determine the nature of this difference. First, we broke down the error scores into the three testing phases, and recalculated the statistics for these phases. The result was that the data were homogeneous for task 1 ($\chi^2 = 39.9$, $df = 54$, $P = 0.937$) and task 2 ($\chi^2 = 64.4$, $df = 54$, $P = 0.157$), but not for the switching phase ($\chi^2 = 283.9$, $df = 234$, $P = 0.014$). A close inspection of the data for all bees immediately showed that this difference was caused predominantly by a single data point: while six bees had no *aborted visits* in the first ten trials of the switching phase, one of the bees had seven such errors during these ten trials! Excluding this bee made the data set statistically homogeneous ($\chi^2 = 213.1$, $df = 195$, $P = 0.179$). For further statistics and in Fig. 2, we therefore pooled the error scores within each group of bees, with the exception of aborted visits for the switching phase in group 2. In the latter data set, the single bee mentioned above was removed.

#### *Group 1 (and the first 100 trials of group 2)*

These bees, which were trained to only one task, started out with almost 40% errors (of both types) during the first ten trials, but their performance rapidly improved, and after about 50 trials, a saturation level below 5% errors was reached (Fig. 2, top, triangular symbols). In the second bin (11–20 trials), performance is already significantly different from random ($\chi^2 = 4$, $df = 1$, $P = 0.045$). If direction errors are evaluated separately, significance from random is even established during the first ten trials ($\chi^2 = 13.3$, $df = 1$, $P = 0.003$) and the error score is actually close to zero after about 100 trials. Most errors from then on are aborted visits (Fig. 2, bottom, triangular symbols). There was no decline in performance overnight.

#### *Group 2*

When bees of group 2 were introduced to the second task, they started out worse (~75% errors during the first ten trials, *aborted visits* and *direction errors* combined; see Fig. 2, top and bottom, gray bold lines) than they had on the first task (~40% errors; Fig. 2, top and bottom, triangular symbols). This result is not surprising, given that these bees had been rewarded 100 times (in addition to the pre-training trial) on the opposite task. In the third bin (21–30 trials), however, the number of correct visits vs. *direction errors* was already distinguishable from random ($\chi^2 = 4.71$, $df = 1$, $P = 0.04$). After 50 trials the bees made no more *direction errors* (Fig. 2, top) and only ~5% aborted visits (Fig. 2, bottom). The total error score reached a significant difference from random in the 6th bin (51–60 visits; $\chi^2 = 11.2$, $df = 1$, $P = 0.0009$).

We then asked if these bees had learned to associate color with direction, or whether they had simply replaced their memory for the task learned first with that for the task on which they had had the second 100 trials. To test this possibility, bees were tested on both tasks with forced alternate trials in the next phase of the experiment (trials 201–600). The result indicates that bees had not learned to associate color with motor pattern (direction) during the first 200 trials: bees started out with ~50% errors during the switching phase. Almost all of these were *direction errors* (Fig. 2, top, black bold line). To test when bees achieved significantly correct directionality, we formed 20 trial bins here, because of the scattered nature of the curve. Testing *direction errors* against correct visits, the curve deviates from random in the second bin (20–40 trials; $\chi^2 = 4.45$, $df = 1$, $P = 0.035$)

We then asked more specifically on which of the two tasks the bees made more errors during the initial part of the switching phase. If there was an interference effect (i.e., if task 1 had been fully or partially forgotten) we expected bees to make fewer errors on task 2 than task 1. This was indeed the case (Fig. 3). We found that, during the first ten trials of the switching phase, bees made almost all their errors on task 1 (36%), and almost none on task 2 (3%). This difference was significant ($\chi^2 = 13.11$, $df = 1$, $P = 0.003$). Interestingly, bees then reversed this trend between 21 and 70 trials; during this phase, they made significantly more errors on the task learned second ($\chi^2 = 4.12$, $df = 1$, $P = 0.042$). Thus, bees simply continued to use the motor pattern learned second during the *initial* 20 trials of the switching phase, irrespective of the color signal. The increased error rates during this phase apparently caused them to reverse their "strategy", and use only the opposite motor pattern (the one learned first) for about 50 trials. Not until this asymmetry disappeared did bee markedly improve their overall performance in the switching phase (Fig. 3). However, at the end of day one, performance was still not in saturation, and the direction error score was still ~20%. During the 200 trials on the second day, bees reached a total error score of ~20%, with only ~10% direction errors (Fig. 2, top, bold black curve).

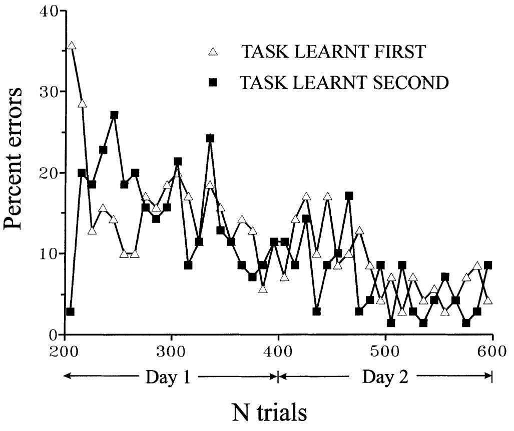

**Fig. 3** Error scores of group 2 in the switching phase, broken down into errors on the task learned first and that learned second. Bees made initially more errors on the task learned first, then on the task learned second, until finally this asymmetry disappeared and overall performance improved

### *Group 3*

Bees of group 3 (those with forced alternate trials from the onset of training) started out no worse than bees trained only on a single task (~20% direction errors, Fig. 2, top, dashed line) but had a slightly higher rate of aborted visits (Fig. 2, bottom, dashed line, see below). Because of the ragged profile of the learning curve, we performed the statistics on bins of 20 trials. There are fewer direction errors than expected by chance during the first 20 visits ($\chi^2 = 6.97$, $df = 1$, $P = 0.008$; Fig. 2, top). Subsequently, a peculiar phenomenon occurred: all five bees had a transient *increase* in direction error rates, so that between 21 and 100 visits, only a single bin of 20 visits (61–80 visits; $\chi^2 = 5.49$, $df = 1$, $P = 0.019$) showed significant (and correct) directionality; in all other intervals (21–40, 41–60, and 81–100 visits) bees chose randomly between the two possible motor patterns ($P > 0.1$ in all cases). Only between 101 and 120 visits was a significant difference from chance again established ($\chi^2 = 5.98$, $df = 1$, $P = 0.014$), and bees then strongly improved their performance, until saturation was reached after ~200 trials, with an overall level of 8% direction errors between 201 and 600 visits. There was a slight increase in direction errors at the onset of the second day, but that was not significant ($Z = 0.89$, $P = 0.372$).

Four of the bees had equal error scores on both tasks throughout the training ($\chi^2 < 73$, $df = 59$, $P > 0.1$ in all cases) but one of the bees made virtually not a single error on the task first introduced until it had accomplished 250 trials; all errors during this time were made on the task that this bee learned second. The overall performance of this bee differed significantly between tasks ($\chi^2 = 112.3$, $df = 59$, $P = 0$). After 250 trials, however, the bee had equal error scores on both tasks ($\chi^2 = 36.2$, $df = 34$, $P = 0.37$).

After completion of the 600 trials during which bees switched between tasks after every visit, the error score (for direction errors) was still 6% (between 500 and 600 trials), and had clearly reached a saturation level by then. The question, then, is, if this relatively poor error score depended on the switch frequency. Would bees perform better if they switched less frequently than after each trial? To answer this question, bees were now forced to switch between the two tasks at random intervals, so that they had between one and ten consecutive trials on one task, then one to ten trials on the second, and so forth. Thus, the overall switch frequency was decreased, but performance did not improve: the error score remained exactly at 6% during this phase of the experiment, and clearly, the difference is not significant ($\chi^2 = 0.1$, $df = 1$, $P = 0.87$, when the error score (direction errors vs. correct visits) in the "random phase" is compared with the last 100 trials of the "switching-after-every-trial-phase"). It is also conceivable that bees only "get confused" immediately after each switch from one task to the other. In that case, they may have higher error scores only on the first visit after a switch between tasks (Woodward and Laverty 1992; Laverty 1994a). However, this was also not the case – the error score (7%) is a little higher for first trials after switches, but not significantly: $\chi^2 = 0.52$, $df = 1$, $P = 0.47$. Thus, once bees had reached a saturation level in terms of error scores, the error frequency was no longer dependent on switch frequency, at least not over the range tested. In addition, this result also shows that, during the first 600 trials, bees had not simply learned that a left turn follows a right turn, and vice versa, instead of associating colors with motor patterns.

### *Comparison between groups – direction errors*

The first general question was whether there would be a decrease in performance if bees had to cope with one on two tasks. To this end, it is useful to compare bees of group 1 (which had learned only one task) with those of the other two groups (which both had learned two tasks). The answer is obvious from Fig. 2 (top): bees of group 1 reached an almost error-free performance after ~100 trials (there were a total of only 23 (<1%) direction errors in the range from 100 to 600 trials), whereas bees of group 3 reached a saturation level only after >200 trials, with 8% direction errors between 200 and 600 trials). Group 2 did not even reach an obvious saturation level until ~500 trials (after which it still had 10% direction errors; Fig. 2, top, black bold curve), but its error score was clearly worse than that of group 1 throughout the entire experiment. In conclusion, those bees that dealt with more than one task clearly incurred increased error rates on the flowers, relative to bees which had learned only one.

In comparing group 2 and 3, we asked whether task switching was detrimental to learning two tasks, or whether continuous switching (as in group 3) might be more efficient than learning both tasks with a blocked schedule (group 2). In a more natural context, the question was whether flower constancy matters during the acquisition phase, in which bees first familiarize themselves with two novel tasks. Recall that bees of group 2 and 3 are exposed to exactly the same procedure during trials 201–600. They are also directly comparable in that they have received equal numbers of trials during trials 1–200 on both tasks. The only difference lies in the sequence of trials: while group 2 had received 100 consecutive trials on each task, group 3 had alternated between tasks from the start.

Figure 2 (top) shows a dramatic difference in performance in the two groups during trials 201–600. Bees of group 2 performed significantly worse than bees of group 3 over this entire range (trials 201–300: $\chi^2 = 127$, $P = 0$; trials 301–400: $\chi^2 = 86.2$, $P = 0$; trials 401–500: $\chi^2 = 45.4$, $P = 0$; trials 501–600: $\chi^2 = 3.91$, $P = 0.048$; $df = 1$ in all cases). Thus, a blocked schedule is inefficient for training bees on two novel tasks.

Next, we asked whether bees of group 2 actually started "from scratch" after trial 200 at the task of associating color with motor pattern. If that were true, their performance during trials 201–300 should equal that of group 3 during trials 1–100. Their performance during trials 301–400 should equal group 3 during trials 101–200, and so forth. This was only partially the case. Indeed, comparing trials 201–300 of group 2 with trials 1–100 of group 3, we found that the difference was insignificant ($\chi^2 = 0.5$, $P = 0.54$). Thus, one might conclude that the first 200 trials in group 2 has just had no effect in terms of the association between color and motor pattern. However, it turns out that this assessment is optimistic. In all subsequent sets of 100 consecutive trials, bees of group 2 performed significantly *worse* than those of group 3 (trials 301–400 of group 2 vs. 101–200 of group 3: $\chi^2 = 9.39$, $P = 0.002$; trials 401–500 of group 2 vs. 201–300 of group 3: $\chi^2 = 34.8$, $P = 0$; trials 501–600 of group 2 vs. 301–400 of group 3: $\chi^2 = 7.08$, $P = 0.008$, $df = 1$, in all cases). Consequently, we infer that bees of group 2 do not start *de novo* at learning the two tasks after trial 200. Instead, the initial training period of 100 consecutive trials actually *slows bees down* at learning to switch between tasks!

The major conclusions from the evaluation of the direction error scores are that (1) bees which specialize on only a single task reach a saturation of performance faster than bees which learn more than one task, and they make almost no errors; and (2) in a foraging context where task switching is favored (e.g., when flowers of two species are morphologically distinct, equally rewarding, and grow intermixed) then switching in the acquisition phase is beneficial for learning two tasks.

### *Comparison between groups – aborted visits*

Aborted visits were most frequent at the start of training on task 1 (almost 20%; group 1 and 2 combined), at the start of task 2 (~30%; group 2), and for those bees which switched from the start (group 3; ~30%; Fig. 2, bottom). On the other hand, all bees of group 2 except one did not show an increase in aborted visits at the start of the switching phase. One of the bees, however, had seven aborted visits during the first ten trials of the switching phase. What is the significance of these errors? One possibility is that bees scent-mark flowers in which they made errors as poorly rewarding, and thus leave such flowers after a brief examination of the entrance tunnel. This may explain why such errors occur predominantly when a novel task is introduced. However, this is unlikely because most direction errors in group 2 occur in the beginning of the switching phase, but only one of the bees showed an increase in aborted visits in this phase. Thus, it is not likely that an increase in direction errors induced the bees to make more aborted visits.

Therefore these increased frequencies of aborted visits at the introduction of each task were likely a delayed response to novel color signals at the entrance. Apparently, bees which had previously been trained, for example, on yellow (left) flowers did not "shy away" from entering the novel blue (right), but then interrupted their visit when the motor memory associated with this new stimulus was not retrievable.

In the saturation phase (401–600 trials) the rate of aborted visits is higher in both groups of bees which switched between tasks (overall percentage 8% in both group 2 and 3) than in the bees which executed only one task (overall percentage 4% in group 1; Fig. 2). This difference is significant (group 1 vs. group 2: $\chi^2 = 32.7$, $df = 1$, $P = 0$; group 1 vs. group 3: $\chi^2 = 8.74$, $df = 1$, $P = 0.003$). Thus, an increased frequency of aborted visits is yet another cost of task switching.

## Handling times

To help visualize the scatter of handling times in our experiments, the raw handling time data for one of the bees of group 2 are given in Fig. 4.

### *Group 1 (and the first 100 trials of group 2, which was given the same treatment)*

Initially, bees were remarkably clumsy at the relatively simple task of navigating a small T-maze: the learning curves (as modeled by exponential decay functions) started at values between 21 and 82 seconds, with an average of 48 seconds (Table 1, Figs. 4–6). However, in all bees, handling times decreased drastically from early to late trials. Saturation levels of handling times $y_0$ ranged from 4.6 to 11.2 s (average 7.9 s, Table 1). The bees reached the 80% criterion between 15 and 77 total trials (average 42 trials). Thus, our T-mazes are comparable in complexity with natural zygomorphic, tubular flowers, where bees reach an 80% criterion after 30–90 trials (Laverty 1994b). We asked if there was a difference between bees which were trained to blue flowers (who had to turn right) and bees trained to yellow flowers (who had to turn left). To answer this question, we compared the parameters of the learning curves $A$, $y_0$ and $t$ of both

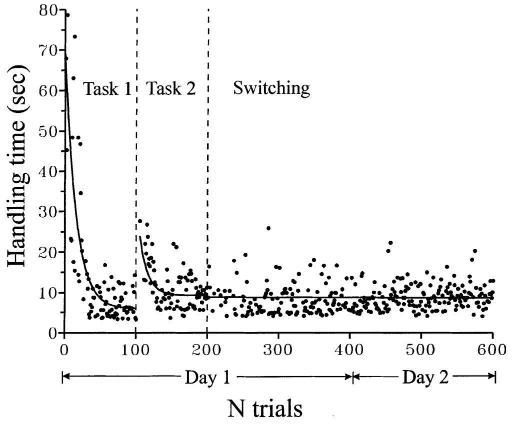

**Fig. 4** Flower handling times for a single bee of group 2, as a function of the number of trials. The *continuous curves* are exponential decay functions fitted to these data, following Eq. 1. Note the transfer effects from task 1 to task 2 (see also Fig. 5, 6, group 2): the bee performed better initially on task 2 than on task 1, but its saturation level on task 2 was worse than the on the task learned first

**Table 1** Learning curve parameters for the handling times of each bee as a function of trials, according to Eq. 1. Bee numbers are given in bold type. In addition, times taken to correct errors, and times taken for transitions between flowers are shown for bees of group 1 and 3. The parameter $y_0$ is the saturation handling time of the trained bee, $A$ the amplitude (the difference between the saturation handling time and the initial handling time of the inexperienced bee); therefore it specifies how much bees improve over training. $A + y_0$ denotes how well bees perform when naive. The parameter $t$ marks the steepness of the curve; it is thus a measure of the speed of learning. The parameter $x_{80\%}$ specifies the number of trials at which the 80% criterion is reached. This criterion is reached when the handling time $y = y_0 + A - 80\% \times A$. When $A$ is very small (i.e., $< 1$, meaning that there is little improvement of the number of trials, and the "learning curve" is horizontal), $t$ will often have arbitrary values; the 80% criterion is not specified in such cases

| | $y_0$ | $A$ | $t$ | $x_{80\%}$ |
|---|---|---|---|---|
| **GROUP 1** | | | | |
| **1** Correct visits | 6.7 | 17.8 | 44.7 | 72 |
| Direction errors | 13.9 | 9.3 | 57.2 | 93 |
| Transitions between fl. | 7.2 | 39 | 6.7 | 11 |
| **2** Correct visits | 9.2 | 49.7 | 23.7 | 39 |
| Direction errors | 10.7 | 48.6 | 65.2 | 105 |
| Transitions between fl. | 5.2 | 22.1 | 8.9 | 15 |
| **3** Correct visits | 8.5 | 25.4 | 47.3 | 77 |
| Direction errors | 16.4 | 23.6 | 43.5 | 71 |
| Transitions between fl. | 6.2 | 12.7 | 11.9 | 20 |
| **4** Correct visits | 8.2 | 58.3 | 16.9 | 28 |
| Direction errors | 12.1 | 47.2 | 26.1 | 43 |
| Transitions between fl. | 10.3 | 34.7 | 15.4 | 25 |
| **5** Correct visits | 10.2 | 59.5 | 24.2 | 39 |
| Direction errors | 14.2 | 69.7 | 30.4 | 49 |
| Transitions between fl. | 6.3 | 22.6 | 19.7 | 32 |
| **6** Correct visits | 5.6 | 30.5 | 12.6 | 21 |
| Direction errors | 12.0 | 23.3 | 160 | 258 |
| Transitions between fl. | 7.4 | 19.6 | 8.6 | 14 |
| **GROUP 2** | | | | |
| **1** Task 1 | 11.2 | 50.6 | 8.7 | 15 |
| Task 2 | 12.5 | 14 | 61.8 | 100 |
| Switch | 17.6 | 0.1 | 930 | – |
| **2** Task 1 | 5.9 | 64.1 | 15.7 | 26 |
| Task 2 | 9.3 | 14.7 | 11.5 | 19 |
| Switch | 8.6 | 0.2 | 517 | – |

**Table 1** (continued)

| | $y_0$ | $A$ | $t$ | $x_{80\%}$ |
|---|---|---|---|---|
| **3** Task 1 | 5.7 | 22.4 | 39.2 | 64 |
| Task 2 | 9.5 | 2.6 | 60.1 | 97 |
| Switch | 9.9 | 0.1 | 38 | – |
| **4** Task 1 | 8.2 | 13.3 | 33.3 | 54 |
| Task 2 | 11.6 | 7.2 | 48.4 | 78 |
| Switch | 9.9 | 0.2 | 597 | – |
| **5** Task 1 | 10.2 | 20.9 | 22.7 | 37 |
| Task 2 | 13.5 | 3.3 | 24.8 | 40 |
| Switch | 12.6 | 0.1 | 127 | – |
| **6** Task 1 | 4.6 | 41 | 23.5 | 38 |
| Task 2 | 16.2 | 4.3 | 60.1 | 97 |
| Switch | 15.4 | 0.6 | 37 | – |
| **7** Task 1 | 8.2 | 74 | 23 | 38 |
| Task 2 | 15.1 | 3.7 | 48.1 | 78 |
| Switch | 15.6 | 0.8 | 12844 | – |
| **GROUP 3** | | | | |
| **1** Task 1 | 10.4 | 67 | 8.0 | 13 |
| Task 2 | 10.7 | 48 | 7.1 | 12 |
| Direction errors | 26.7 | 37 | 28.4 | 46 |
| Transitions between fl. | 6.4 | 89.3 | 7.1 | 12 |
| **2** Task 1 | 10.0 | 49.9 | 6.9 | 12 |
| Task 2 | 8.6 | 42.2 | 8.8 | 15 |
| Direction errors | 20 | 30.8 | 32.7 | 53 |
| Transitions between fl. | 6.7 | 64.1 | 5.7 | 10 |
| **3** Task 1 | 14.9 | 18 | 35.9 | 58 |
| Task 2 | 14.8 | 41 | 22.4 | 37 |
| Direction errors | 22 | 33.8 | 47.5 | 77 |
| Transitions between fl. | 5.2 | 38 | 45 | 73 |
| **4** Task 1 | 10 | 86.4 | 14 | 23 |
| Task 2 | 10.3 | 74.3 | 9.7 | 12 |
| Direction errors | 16 | 123 | 13.9 | 23 |
| Transitions between fl. | 6.2 | 188 | 8.3 | 14 |
| **5** Task 1 | 11.9 | 43.7 | 18.8 | 31 |
| Task 2 | 13.4 | 31 | 13.9 | 23 |
| Direction errors | 21 | 24.8 | 43.8 | 71 |
| Transitions between fl. | 7.2 | 81 | 3.5 | 6 |

Bee number (boldface)

groups of bees by means of a MANOVA. We found that there was no difference in performance between these two subgroups ($V = 0.432$, $P = 0.757$). Finally, there was no difference between the saturation level of day 1 and the average level of day 2 (sign test, $Z = -0.408$, $P = 0.68$). Thus, overnight retention of the handling skill from one day to the next was perfect. This result also means that, in addition to a short term memory, which might have sufficed to explain that skills were memorized from one trial (or one foraging bout) to the next, the motor skills had been stored in long term memory.

### *Group 2*

For the initial 100 trials see the previous section. On the second task, all seven bees of this group started out with shorter handling times than they had had initially on task 1 (Table 1, Figs. 4, 5, middle section, and Fig. 6). This difference was significant ($Z = 2.04$, $P = 0.041$; sign test). Bees started on task 2 at a level which was 22–85% (average 43%) of their initial performance on task 1. Thus, there was a *positive transfer* effect: bees that had learned another task previously were able to use this experience to cope better with the novel task.

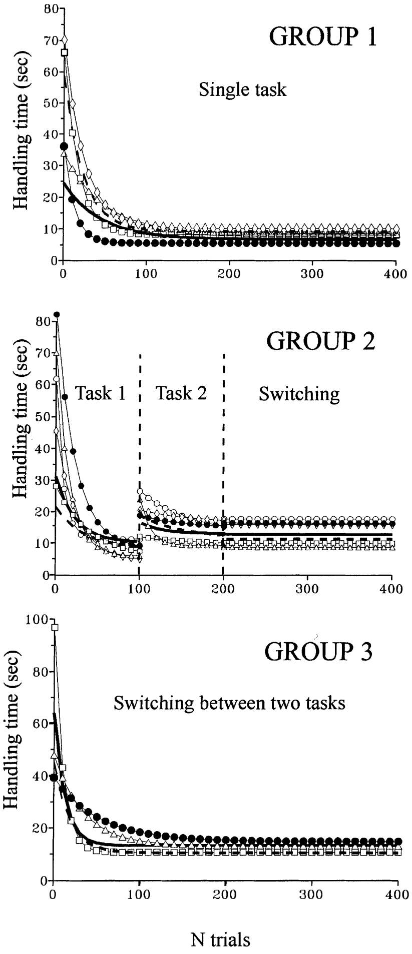

**Fig. 5** Handling times of groups 1–3. Exponential decay functions are given for each individual bee and each learned task. Every *symbol* or *line type* specifies data from one individual bee. Since learning curve parameters did not differ between tasks for group 3, a *joint curve* for both tasks is shown for each bee. Note that the transfer effects in group 2 (as described in Fig. 4) are observable in each individual bee. Despite considerable variation between bees, both groups trained on two tasks (2 and 3) had longer handling times than bees of group 1

In the saturation phase, however, none of the bees became as proficient on the second task as on the first. Saturation levels on task 2 were increased by 12% to 252% (average 79%) relative to task 1. This change was significant ($Z = 2.04$, $P = 0.041$; sign test). Thus, in addition to the positive transfer effect described above, there was also a *negative* transfer effect: bees that had previously stored another task in memory were able to learn a second task, but did not become as efficient at it. It thus appears that the retrieval of the motor memory takes longer when there is more than one option as to which motor pattern to choose. Note that this effect is only observable in the handling times: in terms of error scores, bees reached a practically error-free performance on the second task just as quickly as they had on the first.

In the switching phase (when bees were forced to switch between tasks after each trial), handling times did

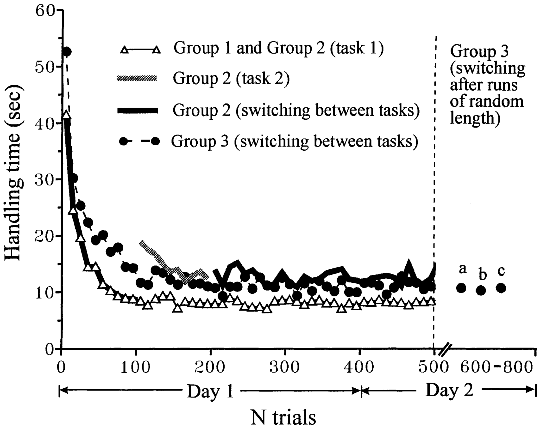

**Fig. 6** Average curves for handling times in all three groups. Each data point is an average of 10 ordered visits from each group. Group 2 received the same treatment as group 1 during the first 100 trials. Therefore, a *joint curve* for both groups is shown for trials 1–100 (*triangular symbols*, *bold segment of curve*). Data produced by group 2 (or to which this group contributed, see above) are denoted with bold lines. Only the first 100 trials are shown for day 2, since there were no apparent changes in behavior during trials 501–600. Both groups (2 and 3) trained on two tasks had longer handling times than bees trained on a single task (group 1) throughout the entire experiment. Right section of figure: average handling times for bees of group 3 during trials 601–800, while bees switched between tasks after runs of 1–10 trials on each task. The precise length of each run was assigned randomly (*a* total average handling time, *b* average handling time of first trials after a switch between tasks, *c* average handling time of trials *not* following a switch). Handling times during this phase did not differ from those while switching was enforced after each trial

not improve from early to late trials (Figs. 4; 5, middle section; and Fig. 6). Instead, handling times remained on the same level that had already been reached in saturation on task 2. There was no significant change between these two phases of the experiment ($Z = 0$, $P = 1$; sign test), nor was there a significant difference between the handling times of the task learned first and that learned second ($Z = 0$, $P = 1$; sign test). It is noteworthy that this is in marked contrast to the error scores in the switching phase of this group: while the error scores were initially close to 50% in the switching phase (indicating that bees had not learned the association between color and motor pattern in the previous phases of the experiment) the motor performance in itself was already in saturation. Thus, while bees were clearly able to perform both motor patterns even at the start of the switching phase (as indicated by evaluation of the handling times), the association between color signals and motor patterns had to be learned anew in the switching phase (as shown by evaluating the error scores). During the switching phase, handling times did not improve to the level of the same bees in the first training phase (when they had learned only a single task). There was no decay in performance from day 1 to day 2 ($Z = 0$, $P = 1$; sign test).

### *Group 3*

These bees started out with handling times of 33–96 s (average 62 s); saturation levels between 8.6 and 14.9 s (average 11.5 s) were achieved, and criterion was reached after 12–58 (average 27) trials on the respective task (Table 1, Fig. 5, lower section; Fig. 6). We asked if learning curves for the task on which bees started differed from that which they had learned second. To this end, the parameters of the learning curve $A$, $y_0$ and $t$ for the two tasks were compared by means of a MANOVA. We found no significant difference between performance on the first and second task ($V = 0.883$, $P = 0.504$). There was also no significant change in average performance from the last ten trials of day 1 to the first ten trials of day 2 ($t$-test for dependent samples $t = 1.21$, $df = 4$, $P = 0.29$).

Finally, we tested whether performance might improve when bees switched at a lower frequency, i.e., at random intervals between one and ten visits on each task. There was no significant difference between saturation handling time during forced alternate trials and average handling time in the random switching phase ($t$-test for dependent samples $t = -1.06$, $df = 4$, $P = 0.345$; Fig. 6, lower section) corroborating what we have stated above in the evaluation of the error scores: once performance is in saturation, it is no longer dependent on switch frequency, in a sense that a decrease in switch frequency might cause an improvement of handling times. We also tested whether handling times might be increased immediately after each switch between tasks. This was done by evaluating the number of instances in which *first* handling times after switches were longer than the *average* handling time of the *subsequent* visits on the same task, before the next switch to another task. This could only be done in cases where the length of each run on the same task was greater than one. There was no significant difference ($Z = 0.35$, $P = 0.723$; sign test). Thus, although we have already identified several cost factors of task switching, increased handling times immediately after task switches are not such a factor.

### *Comparison between groups*

We wished to test if bees which were trained on only a single task performed better or worse than those trained on two tasks. We used planned comparisons by means of one-way between-groups ANOVAs for this purpose.

1. Did bees which started out by learning two tasks (group 3) have longer initial handling times than those bees which learned only a single task (group 1, and group 2 during the first 100 trials)? We tested group 3 against group 1 and group 2 (on task 1) combined. Although the average initial handling time of group 3 (62 s) differed noticeably from that of the other two groups (48 s; Fig. 6), this difference was not significant ($F = 3.49$,

$df = 1$, $P = 0.076$). Thus, we cannot demonstrate that the initial performance is effected by learning either one, or two tasks with alternating trials.

2. We asked if the saturation level of handling times was dependent on whether the bees had stored one or two tasks in memory. We therefore compared the saturation handling time of group 3 (average 11.5 s) with those of group 1 and group 2 during the first 100 trials (average 7.9 s). This difference was highly significant ($F = 15.9$, $df = 1$, $P = 0.0007$). Thus, bees of group 3 were not able to level up to the performance of bees which had learned only a single task (Fig. 6).

3. Did the saturation levels of task-switching bees depend on their training schedule? To answer this question, we tested the saturation levels of group 2 (in the switching phase) against those of group 3. The difference was not significant ($F = 1.08$, $df = 1$, $P = 0.306$). We also asked whether the saturation levels of group 3 differed from those of group 2 during the second 100 trials (when they were trained on task 2). This comparison is necessary to test if the increased handling times of group 3 were actually an effect of switching, or an effect of having learned more than a single option. Bees of group 2 in the second 100 trials did not switch, but they were trained to more than one task. We found no significant difference between these two groups ($F = 0.68$, $df = 1$, $P = 0.42$). Thus, increased saturation handling times occur *whenever* bees are trained to a second task, irrespective of the training schedule, and irrespective of whether the bees are currently switching between tasks or not.

## Learning to correct errors

Since error scores are never actually zero in any of the groups tested (and probably not in nature either), correcting errors is an important capacity that bees should be able to master in order to forage efficiently. Thus, we evaluated the handling times of trials which started out with a direction error (henceforth *correction times*). To see if correction times depended on the number of tasks that bees had learned, we compared group 1 with group 3 (Table 1, Fig. 7).

All bees improved their skills in correcting errors from early to late trials. Initial correction times were not significant between group 1 and 3 (one way between-groups ANOVA: $F = 0.4$, $P = 0.521$); they ranged from 23 to 123 s. Rates of improvement also did not differ between groups ($F = 1.75$, $P = 0.217$), but the saturation levels did ($F = 20.9$, $P = 0.001$). Saturation levels in group 1 ranged from 10.7 to 16.4 s (average 13.2 s), but in group 3 they were substantially higher: 16.0–26.7 s (average 21.1 s). In conclusion, an additional cost encountered by those bees which dealt with more than one task was caused by increased times taken to correct errors.

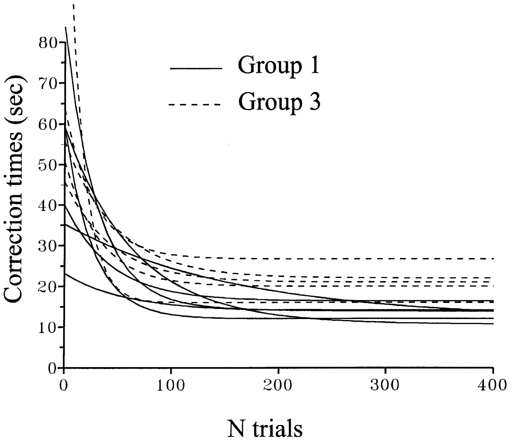

**Fig. 7** Times taken to correct errors by bees of group 1 and 3. Curves are fitted to the raw data according to Eq. 1; each *curve* corresponds to one individual bee. Bees trained on two tasks (group 3) started out at an equal level as those trained on only one (group 1), but had worse saturation levels

## Transitions between flowers

Bees walked between flowers in most cases, probably because their entrances were located level with the floor of the arena, and because they were close together (10 cm distance). Saturation levels of between-flower transition times (times taken to move from one flower to the next) were not different between group 1 and 3 ($F = 0.81$; $P = 0.39$); they ranged from 5.2 to 10.3 s (average 6.8 s) between individuals (Table 1, Fig. 8). Saturation was reached much earlier than for handling times or error scores, usually after <20 trials (Table 1, Fig. 8). Interestingly, the *initial* level of between-flower transitions is much higher for group 3 (43.2–194.2 s, average 98.4 s) than for group 1 (18.9–46.2 s, average 32.2 s, $F = 7.86$, $P = 0.02$). Note that this effect cannot be explained by the distance between flowers: for bees of group 3, flowers of the respective opposite type were always available as nearest neighbors, from whichever type the bee had just emerged. This means that the costs

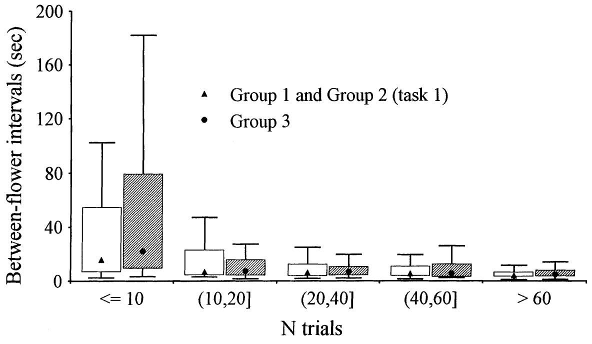

**Fig. 8** Descriptive statistics of the transition times between flowers for bees of group 1 and 3. Symbols (*triangles*, *circles*) specify medians, *boxes* end at the upper and lower quartiles, *whiskers* denote extreme values. Bees which learned both tasks (group 3) started with longer between-visit intervals than those which learned one (group 1), but had equal saturation levels

of task switching concern not only the speed and accuracy of handling flowers, but also concern the transitions between them, at least initially.

## Discussion

A widespread belief in evolutionary behavioral ecology is that animals are often faced with tradeoffs between performing a single task well and several tasks poorly. For example, MacArthur (1972) claimed that "a harvester cannot be simultaneously perfect at several jobs. Perfection in one involves reduced efficiency in another, and if an organism must try to harvest in various ways, it must compromise its efficiency in each." This was written at a time when the "single channel hypothesis" was popular in psychology (reviewed, and criticized, by Allport 1980). This hypothesis, maintaining that humans, at any one time, can only efficiently focus on a single task, has been shown to be invalid for many pairs of tasks (e.g., Annett 1985). Such tradeoffs cannot be assumed *a priori*; they must be explicitly demonstrated.

One reason for the contradictory evidence for temporary specialization in insects may be that several of the previous studies had one (or more) of the following complications: (1) the experience of the animals prior to the experiments was not controlled; (2) numbers and amounts of rewards were not monitored, so that reinforcement and extinction trials were randomly mixed; (3) performance of animals was not measured in a rigorously controlled, automated setup; (4) all failures of animals to accomplish a given task in any given context were conveniently lumped as "learning constraints", without distinctions between motor and sensory learning, short and long term memory, storage and retrieval (see Dukas and Real 1993 for an example that fits all of these points). Our study places controlled experiments on sensori-motor learning into the context of the behavioral ecology of task specialization. In debating the most important effects observed, we will first discuss the implications for bee learning and memory, and then their ramifications for temporary foraging specializations.

### Transfer

Transfer occurs when learning of a behavior in one task influences the learning of a behavior in another (Adams 1987; Schmidt 1991). If the performance of subjects on the task learned second is better than on the first, the transfer is said to be positive; in the opposite case, it is negative. Positive transfer effects have been observed in bee motor learning on natural flowers (Laverty 1994a). We find that bees trained with a blocked schedule had initially shorter handling times on the second task than they had had on the first. Thus, an instance of positive transfer has occurred: we confirm Laverty's observation that bees start out better at handling a second flower species than when they start as entirely naive foragers.

In addition, however, we find a negative transfer effect, which becomes evident only when bees have reached saturation on the second task: the handling times of bees on the second task were increased, on average, by 79% relative to the first. Moreover, all bees which had learned two tasks, independently of training schedule, and independently of switch frequency in the saturation phase, showed this increase, which was maintained over several 100 trials. Fatigue can be excluded as a basis for this phenomenon, because bees of group 1 (those trained on only one task) continued working on its task while group 2 was introduced to the second, but group 1 did not show a decrease in performance during this time. Satiation can also be ruled out as a factor, because freely foraging bees empty their stomach after each foraging bout. What are the reasons for this increase in handling time upon the introduction of the second task?

One possibility is that the motor patterns used in the two flower types are not the same. For example, bees might use some components of the first learned motor pattern for the second flower type. Such behavior was indeed occasionally observed, particularly in bees trained with a blocked schedule. When these bees were trained on the second task, a slight movement towards the previously correct maze arm was sometimes apparent, but then the bee would abort this movement and turn in the correct direction. However, such movements did not occur consistently, and when bees were tested on both tasks, they did not, in general, take longer times on the second task than on the one learned first. It thus appears that the increased times taken to handle the flowers are related to having stored more than a single motor pattern in memory. Delays may be caused by having to retrieve each specific motor pattern from memory, and "uploading" it into a working memory (Honig 1978) so that it can be used in a particular context.

In humans (Adams 1987) as in bees (Laverty 1994a), the degree of transfer (and interference) depends strongly on the specific tasks, as well as the similarity between tasks. It is likely that, had our flowers been differently designed (e.g., if they had been colored on the insides, or if they had had different morphologies), both the shapes of the learning curves and the transfer effects between tasks might have been different. Further experiments with different artificial flower designs are necessary to see if the effects observed here are general properties of sensorimotor learning at flowers, or whether they occur only in some particular pairs of tasks, e.g. when flower designs are very similar, as in our study.

### Interference

Retroactive interference occurs when subjects are trained first on one task, then on a second, and afterwards fail to cope appropriately with task 1 (Adams

1987). Typically, one needs a control group that remains idle while the test group is trained on the second task, and both groups are finally compared in their performance on task 1. Lewis (1986) has used this procedure to test for retroactive interference in butterfly motor learning. Each treatment was given on 1 day, so that the full procedure lasted 3 days. Lewis (1986) found that, indeed, the animals of the test group performed worse than the control group on the last day. However, there is a potential caveat with concluding that this points to interference: the butterflies had no possibility to feed while they were not tested, and so the increased handling times of the test group relative to the control group may simply indicate that members of the latter were more hungry. In fact, Lewis herself points out this difficulty.

Woodward and Laverty (1992) used essentially the same protocol for bumble bees. Since control bees can feed in the nest while they are not tested, different hunger levels can be excluded as confounding the results. It was found that only the first two flower visits on day 3 were above the level of day 1, when bees had foraged on a different species on day 2. Thus, the observed cost is small compared to the initial investments made into learning a novel flower species (Laverty 1994b): the bees had certainly not forgotten what they had learned on day 1.

We show here that interference occurs only when bees are trained in a blocked schedule. When these bees are tested on both tasks after a blocked training on each task, the error scores are initially indistinguishable from random, with most errors made on the task learned first. However, this does not mean that memory capacity is limited to such an extent that only a single task can be stored. The limitation observed here is an effect of the training schedule, not of memory capacity.

An entirely different interference effect is known from honey bee short term memory, which is most sensitive to interference in two time windows: immediately after a trial on the first task ($<30$ s) and then at around 3 min (Menzel 1979). At around 60–100 s, there is an intermediate phase where the memory for the first task is comparatively robust. Menzel concluded that the initial sensitive period marks the time taken to assimilate short term memory, whereas the second marks the transition from short term to a more consolidated form of memory. Interestingly, our bumble bees, when forced to switch between tasks in the learning phase (group 3) adjusted their initial intertrial interval (average: 98 sec, vs. 32 sec. in bees which learned only one task) to the period of low interference sensitivity observed in honey bees. It is thus conceivable that bees take into account this constraint when choosing an interval between trials on two distinct tasks in the learning phase.

## Implications for task specialization

Our data show that, to assess how well animals can cope with several foraging tasks, it is imperative to have tight control over the experience of the tested animals. For example, both groups of bees that were trained on two tasks had time windows in their training schedules where choices are indistinguishable from random. If one observes such animals in nature, one might conclude that they simply cannot deal with more than a single task, which is obviously not the case. In addition, our experiments show that it is not possible to understand performance on any given task without knowing which other tasks the bees have already stored in memory.

What are the inferences of our results for temporary task specialization in foraging bumble bees? Clearly, flower constancy is adaptive, when limitations of sensori-motor learning are taken into account. The best performance is reached by bees that focus on a single task and have learned only a single task. Such bees make practically no errors, and are fast at correcting the few errors they make. They also have the lowest handling times, and their transitions between flowers are initially more rapid (see also Chittka et al. 1997). Similar effects were found in a preliminary study with another bumble bee species (*Bombus occidentalis*; Chittka and Thomson 1996). With all of these limitations in mind, it is not surprising that bees will often restrict their choices to only a few flower species.

However, inconstancy may be favored in certain conditions. In nature, flowers of different species often grow intermixed. Specializing on only one species, then, will imply bypassing other species that are potentially equally or more rewarding (Waser 1986). In theory, learning to handle several species will be favored if the costs imposed by bypassing other species are larger than those imposed by errors and increased handling times. Bees should then be particularly inconstant in the acquisition phase, because they will become proficient at two tasks more quickly if their acquisition phase included switches. Extended runs on single tasks slow the bees down at learning to switch between tasks. However, it is unknown if bees "deliberately" tailor their training schedules to the particular arrays of plants they encounter, or whether the frequency of task switching in the acquisition phase is passively determined by the spatial arrangements of plants of different species.

In the saturation phase, performance does not directly depend on switch frequency, but rather on whether the bee has stored one or two options in memory. This is confirmed by the observation that bees which switch after runs on each task of random length show no change in performance relative to these bees which switch after every trial. Additional support comes from experiments with *Bombus occidentalis*, where bees trained to switch after each trial for 400 trials were then forced to switch only after every two or every five visits. Again, there was no measurable change in performance (L. Chittka and J.D. Thomson, unpublished work). In confirmation of the results of Laverty's (1994a), we find no significant costs immediately after a switch; rather, having to retrieve more than a single motor pattern from memory causes overall handling times to be elevated.

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