

Honey bee foragers as sensory units of their colonies

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Abstract. Forager honey bees function not only as gatherers of food for their colonies, but also as sensory units shaped by natural selection to gather information regarding the location and profitability of forage sites. They transmit this information to colony members by means of waggle dances. To investigate the way bees transduce the *stimulus* of nectar-source profitability into the *response* of number of waggle runs, I performed experiments in which bees were stimulated with a sucrose solution feeder of known profitability and their dance responses were videorecorded. The results suggest that several attributes of this transduction process are adaptations to enhance a bee's effectiveness in reporting on a forage site. (1) Bees register the profitability of a nectar source not by sensing the energy gain per foraging trip or the rate of energy gain per trip, but evidently by sensing the energetic efficiency of their foraging. Perhaps this criterion of nectar-source profitability has been favored by natural selection because the foraging gains of honey bees are typically limited by energy expenditure rather than time availability. (2) There is a linear relationship between the stimulus of energetic efficiency of foraging and the response of number of waggle runs per dance. Such a simple stimulus-response function appears adequate because the range of suprathreshold stimuli (max/min ratio of about 10) is far smaller than the range of responses (max/min ratio of about 100). Although all bees show a linear stimulus-response function, there are large differences among individuals in both the response threshold and the slope of the stimulus-response function. This variation gives the colony a broader dynamic range in responding to food sources than if all bees had identical thresholds of dance response. (3) There is little or no adaptation in the dance response to a strong stimulus (tonic response). Thus each dancing bee reports on the current level of profitability of her forage site rather than the changes in its profitability. This seems appropriate since presumably it is the current profitability of a forage site, not the change in its profitability, which determines a site's attractiveness to other bees. (4) The level of forage-site quality that is the threshold for dancing is

tuned by the bees in relation to forage availability. Bees operate with a lower dance threshold when forage is sparse than when it is abundant. Thus a colony utilizes input about a wide range of forage sites when food is scarce, but filters out input about low-reward sites when food is plentiful. (5) A dancing bee does not present her information in one spot within the hive but instead distributes it over much of the dance floor. Consequently, the dances for different forage sites are mixed together on the dance floor. This helps each bee following the dances to take a random sample of the dance information, which is appropriate for the foraging strategy of a honey bee colony since it is evidently designed to allocate foragers among forage sites in proportion to their profitability.

Key words: *Apis mellifera* – Communication – Foraging – Honey bee – Sensory biology – Waggle dance

Introduction

To respond adaptively to an ever-changing environment, living systems must possess mechanisms for obtaining information about the external world. Metazoan organisms acquire information by means of sensory receptor cells which transduce different environmental stimuli into nervous signals which are then transmitted to the central nervous system. Functionally organized groups of organisms, such as colonies of social insects, also possess special devices for acquiring information. These include individuals devoted to information collection (i.e., scouts and sentinels) and communication processes dedicated to information distribution within the group. Despite the importance of information to successful group functioning, few sociobiological studies have explicitly viewed the properties of individuals as adaptations to provide their group with information about the surrounding environment (see Lumsden and Hölldobler 1983).

This study addresses this gap by analyzing forager honey bees from the perspective that they function not only as food gatherers, but also as sensory units shaped by natural selection to provide their colonies with information about the location and profitability of forage sites. Previous studies have already revealed much about the way in which foragers report on forage sites. For example, it has been known since the classic experiments of von Frisch (1967, see also Gould 1976) that bees transmit this information to hive mates by means of waggle dances. Recent studies of the waggle dance have shown that information about food-source location (direction and distance) is coded in the individual waggle runs of a dance (Michelsen et al. 1992) whereas information about food-source profitability is coded in the total number of waggle runs of a dance (Seeley and Towne 1992).¹ Many questions still remain regarding the performance of foragers as sensory units, however, especially with respect to reporting information about food-source profitability. These can be seen most clearly by noting that to report on food-source profitability a bee first registers the *stimulus* of "food-source profitability" (by integrating information about numerous variables of a flower patch) and then converts this into the *response* of "number of waggle runs". By analogy with cellular sensory units, we can ask the following questions about this stimulus-response relation: What are the units of stimulus intensity? What is the stimulus-response function? Is there sensory adaptation (decline of response to a constant stimulus)? Is there adaptive tuning of the response threshold? How are the responses of the bees organized spatially? The present inquiry addresses these questions for bees reporting on nectar sources and so deepens our understanding of the mechanisms by which a honey bee colony acquires information about the world outside the hive.

Methods

All of the experiments reported here are based on one set of procedures: bees from an observation hive are trained to forage from a sucrose solution feeder whose profitability can be adjusted precisely, the dances of these bees are videorecorded at several settings of feeder profitability, and the videorecords are analyzed to determine the mean number of waggle runs per dance at each setting of profitability. In some experiments it was essential to measure also the energy gained, energy expended, and time spent per forag-

ing trip, so the data needed to calculate these variables were also gathered.

Study site. The experiments were conducted at the Cranberry Lake Biological Station (44°09'N, 74°48'W), in the Adirondack State Park, Saint Lawrence County, in northern New York State. This study site is surrounded by nearly unbroken forests and lakes, hence there are few natural food sources for bees and it is easy to train bees to forage at feeders.

Apparatus. A colony of approximately 4000 Italian honey bees (*Apis mellifera ligustica*) was housed in a two-frame observation hive. To be able to videorecord all dances performed inside the hive, I fitted the hive entrance with a wedge which forced the bees to enter and leave from one side of the comb, and I restricted passage between the two sides of the combs by blocking all side-to-side passageways within 30 cm of the entrance. These measures directed all returning foragers to a well-defined "dance floor" area near the entrance on one side of the hive.

The feeders were designed to provide a sucrose solution with a constant concentration *ad libitum* for 10–30 bees. They were modeled after the feeders described by von Frisch (1967, his Fig. 21). Each one consisted of a 50-ml glass jar containing sucrose solution inverted over a slotted plexiglas plate. This plate-jar combination was placed atop a screened container of anise extract to provide the feeder with scent. Additional scent was provided by mixing 60 µl of anise extract (a 27% solution of essential oil in alcohol) in each liter of sucrose solution.

Dances on the vertical comb of the observation hive were recorded with a video camera (Panasonic WV-3240/12X; VTR NV-8420) positioned so that its field of view encompassed the entire dance floor. The number of waggle runs in each dance was counted during playback (with a videoeditor, Panasonic NV-8950) of the videotapes. The duration of each bee's dance was measured as the total number of waggle runs performed (not the total time spent dancing) during her time in the hive.

Data collection. Each experiment began by training a small group of bees (10–20) out to a feeder located 250–550 m from the hive, and then labelling these bees with paint marks for individual identification. To keep conditions at the feeder as constant as possible, additional bees arriving at the feeder (i.e. recruits) were captured by one assistant stationed at the feeder. Videorecording began after the feeder had been set at the proper level of profitability, the weather conditions had stabilized for the day, and the bees had had 15–30 min (i.e., sufficient time to complete at least two trips to the feeder) to adjust to the feeder's current level of profitability. To ensure accurate identification of the bees during playback of the videotapes, I pointed to each labelled bee as she entered the observation hive and announced her identification colors onto the audio track of the videotape. In several experiments it was necessary also to determine the time budgets of individual bees. This involved measuring the time spent in each of the four segments of a foraging trip: flight out, at feeder, flight in, and at hive. This was accomplished with two additional assistants, one at the hive and one at the feeder, each devoted to recording on audiotape the time of each labelled bee's arrival at or departure from hive or feeder. Subsequent transcription of the two sets of audiotapes yielded a detailed record for each bee of the time length of each segment of each foraging trip. To measure how much sucrose solution each bee loaded on each foraging trip, we weighed each bee to the nearest milligram with a torsion balance when she arrived at the feeder and again when she started to fly back to the hive (for details of this procedure, see Seeley 1986, p. 344). The difference in these weighings indicates the weight of solution imbibed. The volume of solution loaded was subsequently calculated using standard data on the densities of sucrose solutions (CRC Handbook of Chemistry and Physics; the air temperature varied by less than 5° C during the collection of the weight data, hence no allowance was made for change in sucrose solution density due to change in temperature). Because the handling needed to weigh

¹ It should be noted that although bees performing dances do code food-source profitability in the number of waggle runs in a dance, the bees following dances do not actually perceive (decode) this parameter of a dance and do not compare the number of waggle runs in the dances of different bees (Seeley and Towne 1992). Nevertheless, the positive correlation between food-source profitability and number of waggle runs is an important property of this communication process, because the larger the number of waggle runs in a bee's dance, the greater the duration of her recruitment signal, and the more recruits she arouses. Thus the grading of waggle-run number in accordance with food-source profitability results in a higher per capita rate of recruitment by bees from richer food sources relative to that of bees from poorer food sources, and this helps a colony keep its foraging efforts focused on the best available sources of food

bees altered the time course of their foraging and could have affected their dancing, we always collected the weight data on the day following the day on which we recorded dances and measured foraging times.

Energetic calculations. The gross energy gained per bee per foraging trip (G , in joules) was calculated as follows:

$$G = V \cdot S \cdot 5.8$$

where V is volume of sucrose solution loaded on the trip (in μl), S is the concentration of the sucrose solution (in mol/l, or $\mu\text{mol}/\mu\text{l}$), and 5.8 is the standard value for the energetic equivalence of sucrose, (in J/ μmol , Kleiber 1961).

The energy expended per bee per foraging trip (C , in joules) was calculated by using metabolic rates to convert the time budget of a trip to an estimate of energy consumption, as follows:

$$C = \sum_{i=1}^4 T_i \cdot MR_i$$

where i denotes the segment of a foraging trip (1=flight out, 2=at feeder, 3=flight in, 4=at hive), T_i is the duration of segment i (in s), and MR_i is the metabolic rate of the bee during segment i (in J/s). The metabolic rate for each segment was determined separately for each bee using the allometric equations determined by Wolf et al. (1989) from measurements of rates of oxygen consumption. Because the respiratory quotient of honey bees is nearly 1.0 (Rothe and Nachtigall 1989), these allometric equations for rates of oxygen consumption (ml O_2/h) could be directly converted to equations for rates of energy consumption (J/s), using the conversion factor that 1 ml O_2 corresponds to 20.1 J. The converted equations are as follows: *flying bees* (segments 1 and 3), $MR = 0.00287 \cdot M^{0.629}$; *walking or motionless bees* (segments 2 and 4), $MR = 0.00248 \cdot M^{0.492}$, where MR is the metabolic rate (J/s) and M is the body mass (including nectar load) (mg).

Results

What are the units of stimulus intensity?

A crucial first step in the analysis of any sensory system is to determine what natural selection has shaped the sensory system to measure and report. In the present case of bees reporting on nectar-source profitability, we need to determine what the bees measure when assessing a nectar source. In other words, what is the bees' criterion of nectar-source profitability? The procedure used to answer this question was to (1) train a group of 20 bees to each of two feeders at different distances (250 and 550 m) from the hive, (2) determine a concentration of sucrose solution for each feeder such that the bees judged the feeders equally profitable (indicated by the two groups performing the same mean number of waggle runs per dance), and finally, for the conditions that elicit equal dancing, (3) calculate the profitability of each feeder according to various hypothetical measures of profitability. If any one of these measures yields equal values for the two feeders, then this suggests that this hypothetical measure is a good approximation of the bees' actual measure of nectar-source profitability. The three measures of profitability that were considered were the three alternative foraging "currencies" that are most often evaluated in studies of animal foraging behavior: net energy gain ($G - C$), net rate of energy gain [$(G - C)/T$], and net energy efficiency [$(G - C)/C$], where G = gross

energy gain, C = costs involved in foraging, and T = time spent foraging.

Both trials of this experiment were begun in the morning with the far (550 m) feeder filled with a 2.50 mol/l sucrose solution, and the near (250 m) feeder filled with a 1.75 mol/l sucrose solution. As is indicated in Table 1, analysis of the dance records indicated a higher mean number of waggle runs per dance for the near feeder in both trials, yielding a dance ratio of 1.57 (far-feeder value/near-feeder value) in both instances. Then, during the afternoon of both trials the far feeder was left at 2.50 mol/l and the near feeder was switched to 1.25 mol/l. Dance measurements now indicated a lower mean number of waggle runs per dance for the near feeder in both trials, yielding dance ratios of 0.89 and 0.58. By linearly interpolating between the results from the morning and afternoon, I estimated for each trial a concentration of sucrose solution for the near feeder that would elicit dances with the same mean number of waggle runs as in the dances for the far feeder, or in other words a dance ratio of 1.00. This was 1.32 and 1.46 mol/l for the first and second trials.²

Table 1 presents a summary of the measurements of bee weights, the measurements of duration for different segments of foraging trips, and the estimates of various energetic variables, all for conditions close to those that elicited equal dancing for the two feeders. It shows that the net energy gain per foraging trip was extremely different for the near and far feeders (paired t -test, $t = 12.73$, $df = 1$, $P < 0.05$). Likewise, the net rate of energy gain was significantly different for the two feeders (paired t -test, $t = 17.00$, $df = 1$, $P < 0.05$), although here the difference was not nearly so pronounced as for net energy gain. However, the net energetic efficiency did not differ significantly for the two feeders (paired t -test, $t = 1.18$, $df = 1$, $P > 0.40$) under conditions that elicited equivalent dancing. Obviously the bees did not measure

² This experimental procedure assumes that it is valid to compare the dance ratios observed in the morning and afternoon. In particular, it assumes that the change in the dance ratio for the two feeders between morning and afternoon was caused solely by the change in the sugar solution at the near feeder, and not at all by such things as changes in the weather conditions. This assumption may seem questionable because in both trials there was a noticeable increase in the dancing for the far feeder between morning and afternoon, even though its sugar solution had not been changed, probably because the air had warmed and so the foraging conditions had improved. In previous studies, however, I have observed that even though the *absolute* duration of the dances for two unchanging feeders sometimes does change markedly between morning and afternoon, the *relative* duration of the dances does not change so strongly between morning and afternoon. Consider, for example, the results reported in Table 2 of Seeley and Towne 1992, for 7 July 1990. Between 10:04 a.m. and 12:22 p.m., 36 dances were measured for each of two groups of foragers from one colony, with one group of foragers visiting a 2.5 mol/l feeder and the other visiting a 2.0 mol/l feeder, both 400 m from the hive. The mean number of waggle runs per dance for these two forager groups was 3.83 and 2.19, giving a dance ratio of 1.75. Between 12:26 and 14:31 p.m. another 36 dances were measured for each group of bees, and the mean number of waggle runs per dance for the two groups had risen to 5.50 and 3.08, but the dance ratio was essentially unchanged at 1.78

Table 1. Results of the experiment analyzing the bee's criterion of nectar-source profitability

	Trial 1: 15 July 1992			Trial 2: 17 July 1992		
	Near feeder	Far feeder	Ratio	Near feeder	Far feeder	Ratio
Waggle runs/trip						
a.m. (N: 1.75, F: 2.50) ^a	11.0 ± 2.0	7.0 ± 1.8	1.57	8.8 ± 1.1	5.6 ± 1.2	1.57
p.m. (N: 1.25, F: 2.50)	10.1 ± 1.7	11.4 ± 2.0	0.89	4.7 ± 1.1	8.1 ± 1.3	0.58
Sucrose solutions for equal dancing (mol/l)	1.32	2.50		1.46	2.50	
Bee weights (mg) ^b						
Empty	75 ± 1	78 ± 1		75 ± 1	76 ± 1	
Full	131 ± 2	144 ± 2		133 ± 2	142 ± 2	
Mean load volume (µl)	47	50		49	50	
Mean gain per trip (J)	360	725		415	725	
Mean trip segment times (s) ^c						
Flight out	41 ± 1	86 ± 2		40 ± 1	70 ± 2	
At feeder	60 ± 4	110 ± 5		53 ± 4	93 ± 4	
Flight in	42 ± 0	98 ± 3		40 ± 1	70 ± 2	
At hive	103 ± 6	146 ± 6		90 ± 4	126 ± 5	
Total trip	246	440		223	359	
Mean cost/trip (J)	7.8	15.7		7.2	12.3	
Possible criteria						
Gain-Cost (J)	352	709	0.50	408	713	0.57
(Gain - Cost)/Time (J/s)	1.43	1.61	0.88	1.83	1.99	0.92
(Gain-Cost)/Cost (J/J)	45.1	45.2	1.00	56.7	57.9	0.98

^a N = near feeder, F = far feeder. The associated numbers specify the concentration of the sucrose solution, in mol/l, at each feeder. Each value of "waggle runs/trip" represents the mean of 60 measurements of dance duration ($\bar{x} \pm SE$)

^b Weight data were gathered with bees collecting a 1.50 mol/l sucrose solution at the near feeder and a 2.50 mol/l solution at the far feeder. These data were gathered on the day after the data on dancing were gathered. Each value of "bee weight" represents the mean of at least 20 measurements ($\bar{x} \pm SE$). The difference between the mean weights of empty and full bees (in mg) was converted to a mean nectar load (in µl) volume by dividing by the appropriate solution density: 1.20 and 1.31 mg/µl for the 1.5 and 2.5 mol/l sucrose solutions, respectively

^c Time data were gathered with bees collecting a 1.25 or 1.75 mol/l sucrose solution at the near feeder and a 2.50 mol/l solution at the far feeder, simultaneous with the collection of the dance data. Since none of the means differed for the 1.25 and 1.75 mol/l solutions, the data were pooled and the overall means for each trip segment (shown) were used in the calculations. The "at feeder" and "at hive" times differ markedly between the near and far feeder bees, evidently because of the strong difference in viscosity of their sugar solutions, which influences the time required to load and unload the solutions. Each value of "trip segment time" represents the mean of at least 30 measurements ($\bar{x} \pm SE$)

the profitability of the feeders by sensing the energy gain per trip to a feeder, and it seems doubtful that they did so by sensing the rate of energy gain during foraging. Instead, these results suggest that bees registered the profitability of each feeder by sensing the energetic efficiency of their foraging. Therefore I use energetic efficiency as the criterion of feeder profitability in the following sections.

What is the stimulus-response function?

To investigate the way in which individual bees grade their dance response in relation to the stimulus of nectar-source profitability, bees were stimulated with a feeder containing an increasingly concentrated sucrose solution and their dance responses were videorecorded. Data on bee weight and trip segment duration were also collected so that the profitability experienced by each bee at each level of sugar concentration could be determined. All dance and trip time data were gathered on 29 June 1992, while the data on bee weight were collected on the following day.

The feeder was positioned 350 m from the hive and was successively loaded with a 1.50, 2.00, or 2.50 mol/l sucrose solution for 90 min each. The first 30 min at each setting gave the bees time to adjust to the conditions; the remaining 60 min gave us time to collect data. Seven labelled bees visited the feeder regularly, making 12.2 ± 2.2 trips to the feeder during each 60-min period of data collection. The dance response of each bee as a function of the feeder profitability that she experienced is shown in Fig. 1; the results of regression analyses (model II regression, Sokal and Rohlf 1981, p. 547) are presented in Table 2. Different bees experienced different profitabilities for the same sucrose solution (because they differed in the amount of solution loaded, in body weight, and in foraging tempo) and danced to different extents, even for the same general level of profitability. An analysis of covariance showed significant variation in slope of regression lines among the seven bees ($F = 18.31$, $P < 0.001$). However, all of the bees showed a clearly linear relation between profitability and dance response.

To understand the rationale of this linear relationship between stimulus and response (as opposed to, say, a

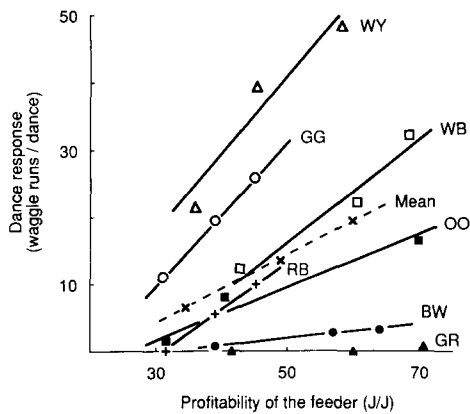


Fig. 1. Stimulus-response functions for seven bees reporting on a sucrose-solution feeder of variable profitability. Each bee made approximately 12 trips to the feeder at each of three different stimulus levels (feeder profitability, measured in units of energetic efficiency) and at the end of each trip produced a dance response, which was videorecorded. All of the bees showed a simple, linear relationship between stimulus and response, though the individual bees (*different symbols*) differed significantly in the slopes of their regression lines relating stimulus and response. Experiment conducted on 29 June 1992

logarithmic relationship), it is useful to consider the magnitude of variation for both stimulus and response. A prior study of dances for natural food sources shows that the dance response can range from 1 waggle run to about 100 waggle runs (Seeley and Towne 1992), hence the response range (maximum/minimum) is about 100. To estimate the range of stimuli to which the bees respond, I have used the regression lines for the Fig. 1 data to estimate each bee's threshold and maximum stimulus values, that is, the levels of nectar-source profitability that will elicit 1 and 100 waggle runs. The results, shown in Table 2, vary considerably from bee to bee. Nevertheless, these calculations reveal a rather consistent stimulus range (maximum/threshold) of 5–20. (One bee – GR – deviates from this, but she responded (danced) so weakly that her stimulus-response function could not be determined with precision). Given that the range of stimuli that elicit responses (approx. 10) is far smaller than the range of responses (approx. 100), a sim-

ple, linear stimulus-response function seems adequate for coding information about nectar-source profitability (see Discussion).

Is there sensory adaptation?

Sensory receptor neurons often exhibit adaptation – decreased response over time to a constant stimulus – as a means of improving their ability to report stimulus changes. To determine whether bees functioning as sensory units also exhibit adaptation, a group of bees was exposed to prolonged stimulation with a feeder with high profitability, and the bees' dance responses were recorded.

In this experiment ten bees were allowed to forage from a feeder located 350 m from their hive. The bees were exposed initially to a weak stimulus for 1 h (feeder filled with 1.00 mol/l sucrose solution), then to a strong stimulus (feeder refilled with 2.50 mol/l sucrose solution) for 2 h, and finally to the weak stimulus for 1 h more. Two trials of the experiment, performed on consecutive days, yielded essentially identical results. Figure 2 illustrates the results of one trial. It shows no sign of adaptation to the strong stimulus. This is seen most clearly in the summed response of the ten bees, where one sees a slight *increase* in the collective dance response over the 2 h period of strong stimulus (regression line: $Y = 0.99 \cdot X + 239.6$; the slope is not quite significantly different from zero, with $P = 0.078$). From a baseline response to the weak stimulus of 113 ± 17 waggle runs per 15 min, the response rose during the first 30 min of strong stimulus to 236 ± 41 waggle runs per 15 min and continued to rise, reaching 314 ± 34 waggle runs per 15 min during the last 30 min of strong stimulation ($\bar{x} \pm SD$). This rise, if genuine, may be due to a small change in the foraging conditions (air temperature, nectar influx from natural sources?) over the course of the experiment. One indication that the foraging conditions had changed slightly is the somewhat higher level of dancing to the weak (control) stimulus at the end of the experiment (161 ± 42 waggle runs total per 15 min) compared to the start of the experiment (113 ± 17 waggle runs per 15 min; $P < 0.09$).

Table 2. Results of regression analyses of the profitability-dance relations shown in Fig. 1, together with an estimate of the threshold and maximum levels of stimulus for each bee

Bee	Regression line	r^2	Stimulus (J/J) ^a		
			Threshold	"Maximum"	Ratio
WY	$Y = 1.16 \cdot X - 17.7$	0.91	16	102	6.4
GG	$Y = 1.06 \cdot X - 21.7$	1.00	21	115	5.5
WB	$Y = 0.75 \cdot X - 21.2$	0.95	30	162	5.4
RB	$Y = 0.73 \cdot X - 23.1$	1.00	33	169	5.1
OO	$Y = 0.39 \cdot X - 10.1$	0.96	28	285	10.2
BW	$Y = 0.11 \cdot X - 3.4$	1.00	40	940	23.5
GR	$Y = 0.01 \cdot X - 0.6$	0.60	160	10060	62.9
Mean	$Y = 0.51 \cdot X - 11.1$	1.00	24	218	9.1

^a Each bee's stimulus values were estimated from its regression line. The threshold and "maximum" stimuli were calculated as those which would elicit 1 waggle run or 100 waggle runs per dance, respectively

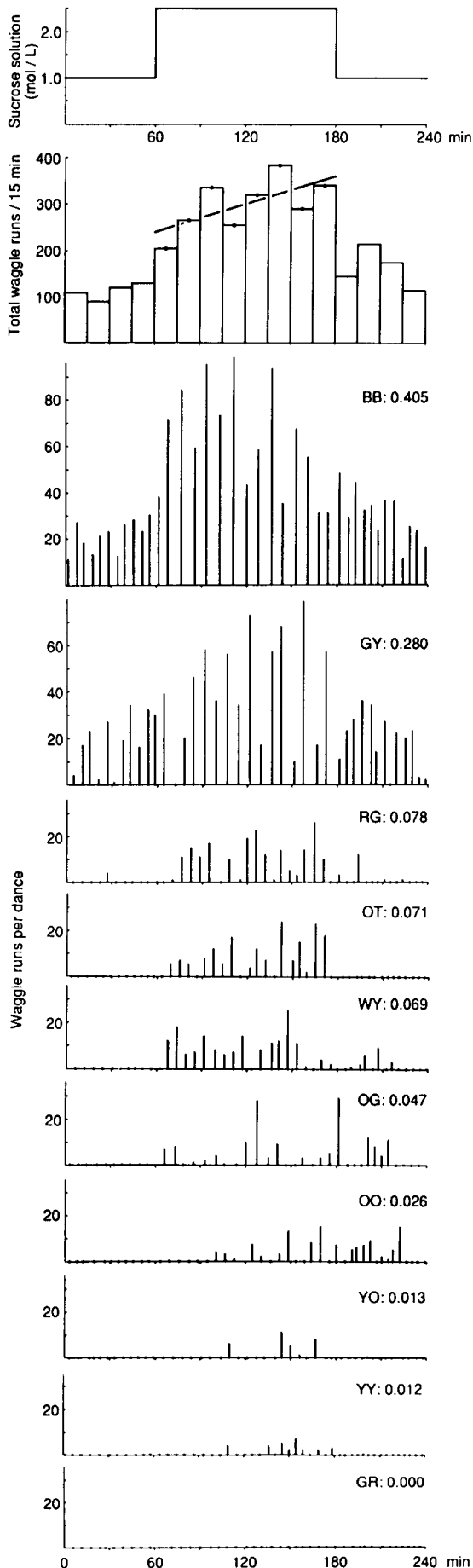


Figure 2 also underscores one of the messages derived from Fig. 1, namely large variation among bees in dance response to a given stimulus of food-source profitability. This can be seen qualitatively in terms of different dance thresholds. For two of the ten bees (BB and GY) even the 1.00 mol/l feeder provided a stimulus that was above threshold, while for seven more bees only the 2.50 mol/l feeder gave a suprathreshold stimulus, and the remaining bee (GR) evidently required a still higher stimulus to elicit dancing. (Note: three of the bees represented in Fig. 2 – WY, 00, and GR – are also represented in Fig. 1. Hence these two figures present independent, consistent pictures of the differences in dance threshold among these three bees). A more quantitative assessment of the variation among bees is provided by an analysis of variance. When applied to the dances recorded during the 2 h of strong stimulus, it reveals highly significant heterogeneity among the mean dance durations of the ten bees ($P \ll 0.001$), with 74% of the total variation in dance duration due to variation among bees and only 26% due to variation within bees. One effect of this large variability in dance response among bees is that the majority of the reporting about food sources may be done by a small minority of the foragers. In this particular experiment, for example, 85% of the waggle runs for the weak stimulus and 68% of the waggle runs for the strong stimulus were produced by only 20% of the bees (BB and GY).

Is there adaptive tuning of the response threshold?

There is little doubt that bees adjust the dance threshold in relation to foraging conditions, such that the greater the forage abundance the higher the threshold level of food-source profitability (Lindauer 1948; Seeley 1986). This adjustment has the effect that bees report low-yield sources only when necessary, that is, when food is scarce. An explicit documentation of this tuning of the dance threshold has never been made, however. To accomplish this, I present a reanalysis of results from an experiment already reported in Table 2 of Seeley and Towne 1992. In this experiment we provided a colony with two feeders of different profitability simultaneously and measured the mean duration of the dances for each feeder. These

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Fig. 2. Durations of dances produced by ten bees responding first to a weak, then to a strong stimulus. The stimulus intensity was varied by changing the concentration of the sucrose solution in a feeder according to the schedule shown in the *top panel*, and each bee's dance responses were measured from videorecords. The summed response of the ten bees shows no sign of adaptation (reduced response), even after 2 h of strong stimulation. The separate responses of the ten bees differ significantly in their mean values (analysis of variance: $F_{10, 210} = 58.9$, $P \ll 0.001$). *Letters on the right* denote individual bees; the *number* beside each bee's *identification code* denotes the proportional contribution of each bee to the total waggle runs produced by all ten bees during the 2 h period of strong stimulus. Note that the majority of the dances for the feeder were produced by a small minority of the bees. Experiment conducted on 16 June 1992

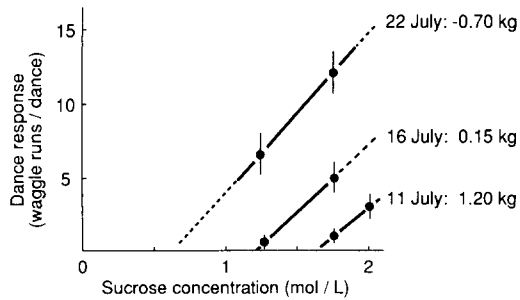


Fig. 3. Dance response as a function of sucrose concentration on three days with very different foraging conditions. *Numbers on the right* denote the daily weight change of a beehive mounted on scales, which provides a measure of the nectar availability each day. As the foraging conditions deteriorated, the bees lowered the threshold concentration for dancing but they did not change the slope of the stimulus-response line. Based on data originally reported in Seeley and Towne (1992)

measurements, made over the course of a day, revealed the profitability-dance function for that day (Fig. 3). The experiment was repeated 11 times over a 24-day period, during which time the foraging conditions changed greatly. When the experiment began in early July, there was a light nectar flow from wild raspberry plants (*Rubus* spp.), but by the end of the experiment in late July, the raspberry bloom had passed and there was virtually no nectar available except the artificial nectar in our feeders. The availability of natural forage was assayed daily by measuring the weight change of a colony on scales.

Figure 3 shows the stimulus-response functions for three days with very different foraging conditions, ranging from good (11 July) to bad (22 July). Analysis of covariance of the results illustrated here indicates that although the slopes of the functions do not differ ($P > 0.25$), there is significant heterogeneity of the means ($P < 0.005$). This implies that the dance response differed significantly on the three days when sugar concentration is kept constant. Evidently, as the foraging conditions deteriorated over the period 11–22 July, the bees did not radically change the form of their stimulus-response function, but simply lowered the threshold of response.

How are the responses of the bees organized spatially?

Single dances. When a bee returns to the hive and reports on her food source, she does not present her information in one spot but instead broadcasts it over much of the dance floor. This is illustrated in Fig. 4A (note: the size of the dance floor is depicted in Fig. 5). Analyses of the videorecords of dances by bees visiting a sucrose-resolution feeder indicate that this dispersion of dance information arises as a result of the following three spatio-temporal characteristics of dances.

First, dances with many waggle runs are performed not as one continuous string of waggle runs, but as several bouts of dancing punctuated by breaks lasting a few seconds. Analysis of ten long dances (i.e., ones with

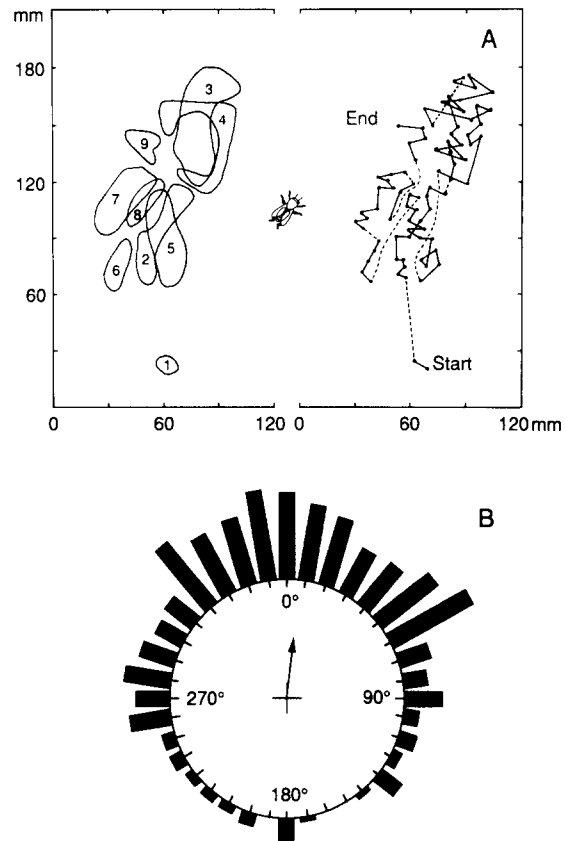


Fig. 4A, B. Travel pattern of a dancing bee. **A** Spatial distribution on the dance floor of 81 waggle runs produced during a single dance. Each *dot* on the *right side* of the figure marks the position of the bee's thorax at the start of a waggle run. *Solid lines* connect the waggle runs within a continuous bout of dancing; *dashed lines* connect the last and first waggle runs of two consecutive bouts of dancing. The *numbered forms* on the *left side* of the figure outline the areas swept out during each of the nine bouts of dancing which constituted the complete dance. The bee in the *center* (drawn to scale) shows the orientation of the waggle runs in this dance. **B** Circular distribution of the direction of displacement between waggle runs relative to the direction of the waggle runs (0° = travel in the same direction as the waggle runs), as measured for 273 inter-waggle-run displacements from 5 dances. Between waggle runs, the dancing bee tends to move in the same general direction as the waggle run [mean orientation vector (r) = 0.49 at 4° ; Rayleigh test: $z = 65.2$, $P < 0.001$]

69.3 ± 12.2 waggle runs, range 55–93) revealed that these dances were broken into 5.5 ± 2.9 bouts, with 12.5 ± 12.3 waggle runs per bout ($n = 55$ bouts). The pauses between bouts were spent either unloading nectar to a nearby bee, or walking to a new location on the dance floor, or both. Short dances, those with fewer than 15 waggle runs, generally are completed in just one bout of dancing ($P = 0.73$, $n = 30$ short dances).

Second, within a single bout of dancing (in both long and short dances) the individual waggle runs are not superimposed. Rather, consecutive runs are offset from one another by a few millimeters (8.0 ± 4.8 mm, $n = 747$ inter-waggle run distances from 18 dances). This displacement arises because the dancing bee, upon finishing one waggle run and circling back to start another, rarely travels all the way back to the starting point of the pre-

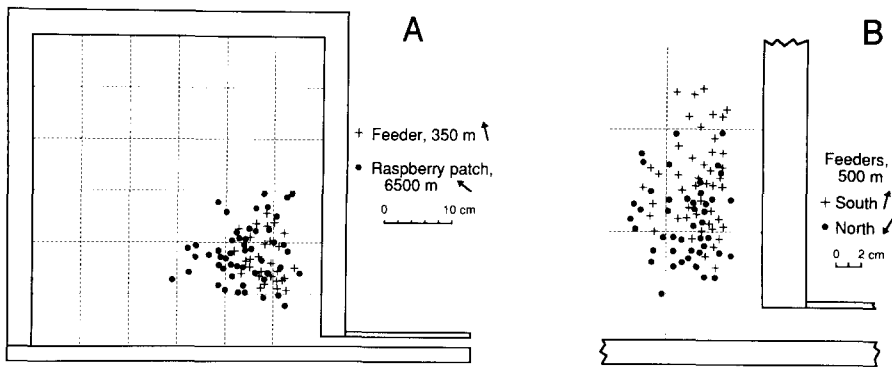


Fig. 5 A, B. Spatial distributions of dances for two widely separated forage sites. Dances were plotted in an observation hive during scan samples made at 2-min intervals over a 20-min period. *Arrows* at the *right* specify the direction of the waggle runs for the dances of each site. Dates of data collection: **A** 29 June 1992; **B** 18 July 1992. In both **A** and **B**, there is broad overlap between the two

sets of dances but also a small, statistically significant difference in their mean locations. It seems likely that this difference is without functional significance and is simply an incidental effect of the tendency of dancing bees to drift across the dance floor in the direction of their dancing

vious waggle run. Hence, in executing a bout of dancing, a bee slowly drifts across the dance floor, moving in the same general direction as she steers her waggle runs (see Fig. 4B).

Third, there is displacement between bouts of dancing. The average distance between the final waggle run in one bout and the first waggle run in the next bout is 34.1 ± 24.0 mm ($n=45$). This distance is significantly greater than that between waggle runs within a bout ($P < 0.001$) and, as is illustrated in Fig. 4A, it contributes heavily to the dispersed presentation of dance information.

Multiple dances. At any given time, the dances in a hive will generally represent several distinct forage sites separated by hundreds if not thousands of meters. How is this information about spatially segregated sites mapped onto the dance floor? Is there a clear spatial separation of dances for different sites, or are dances for different sites mixed together at random? Evidently neither of these two extreme possibilities matches reality. Consider the results in Fig. 5A, which shows the locations of dances for two sites spaced more than 6 km apart. On the one hand, there is no clear-cut spatial segregation of the two sets of dances, but on the other hand, there is a small, statistically significant difference between the two sets in horizontal distance from the hive entrance: feeder, 9.2 ± 2.5 cm; raspberry patch, 12.6 ± 4.8 cm ($P < 0.001$). This difference evidently arose because of the within-dance drift described above, which resulted in the bees dancing for the raspberry patch drifting to the left and the bees dancing for the feeder drifting upward. This explanation derives additional support from the results illustrated in Fig. 5B. Here the two forage sites were in opposite directions from the hive, hence the waggle runs representing them were oriented in opposite directions (roughly speaking, downward for the north feeder and upward for the south feeder), and the two dance distributions differed slightly in mean vertical distance from the hive floor: north feeder, 8.8 ± 3.0 cm;

south feeder, 12.0 ± 3.6 cm ($P < 0.001$). It is important to also notice, however, that here again the spatial distributions of the two sets of dances overlap broadly.

Discussion

The criterion of nectar-source profitability

“The mind makes the world in which it lives” (Wilson 1971, p. 197). To investigate how the mind of a bee defines nectar-source profitability, I created two sucrose solution feeders that differed in sucrose concentration and distance from the hive but elicited dancing at the about same intensity, then measured the mean energy gain, energy cost, and time per trip to each feeder, and finally determined what mathematical configuration of these variables would yield the same value for the two different nectar sources. The answer turned out to be net energetic efficiency, that is, $(\text{gain} - \text{cost})/\text{cost}$. Furthermore, when bees were allowed to forage from a sucrose solution feeder whose profitability could be adjusted, and the waggle dances of individual bees were measured for the different settings of feeder profitability, it was found that each bee precisely scaled her dance output as a linear function of net energetic efficiency. Thus it appears that the nervous system of worker bees is designed to rank the profitability of nectar sources according to the criterion of energetic efficiency. This conclusion is consistent with the work of Waddington (1985), who found that the vigor (reversal rate) of round dances correlates with the gains and costs of exploiting a feeder in a way that suggests that bees assess a feeder’s profitability in terms of a ratio of gain to cost.

Why has natural selection apparently favored the energy efficiency criterion over others, such as rate of energy delivery to the hive? One possible explanation is suggested by recent empirical and theoretical work (Schmid-Hempel et al. 1985; Schmid-Hempel 1987; Kacelnik et al. 1986; reviewed by Schmid-Hempel 1991). This

work shows that if a bee's foraging gains are limited not by time but by energy expenditure (either daily, *sensu* Drent and Daan 1980, or lifetime, *sensu* Neukirch 1982; Wolf and Schmid-Hempel 1989), then a bee will actually maximize her total energy delivery to the hive by maximizing energy delivery per unit of expenditure, i.e., by maximizing energetic efficiency.

Now consider what a nectar forager must do to maximize energetic efficiency. First she must locate a forage site where the potential for efficient foraging is as high as possible, then she must behave in a way that maximizes the efficiency of her foraging at this site. A bee surmounts the first of these two hurdles by following a recruitment dance to locate a forage site (Lindauer 1952; Seeley 1983). This works because, as we have seen (Fig. 1), recruitment dances are graded in strength according to the criterion of foraging efficiency, hence a forager is most likely to be recruited to a site offering highly efficient foraging. Once a forager has been recruited to such a site, she then overcomes the second hurdle to efficient foraging by appropriately adjusting her foraging behavior at the site. For example, nectar foragers often cease gathering nectar and return to their hive before they have acquired a full load of nectar. At first thought this seems like a highly maladaptive behavior, but energetic analyses indicate that this strategy of partial loading helps a bee maximize the energetic efficiency of her foraging, since it can greatly reduce the energy expended on a foraging trip (Schmid-Hempel et al. 1985, Schmid-Hempel 1987; Kacelnik et al. 1986). Hence several different lines of study provide consistent indications that nectar foraging honey bees seek to maximize the efficiency of their colony's nectar collection.

A final cautionary note must be added, however. There is a good possibility that nectar foraging bees do not have a fixed maximization goal, but instead seek to maximize different things at different times of the year and under different colony conditions (for a general discussion, see Schmid Hempel et al. 1993). Consider two hypothetical examples. First, nectar-foraging bees in autumn may seek to maximize the rate of energy deliv-

ery to the hive, rather than the efficiency of this energy delivery, since their foraging gains are severely limited by the time available before cold winter weather arrives. Such rate maximization may prove especially clear for foragers in colonies that have not yet accumulated sufficient honey to survive winter. Second, nectar-foraging bees in small colonies may seek to maximize the rate of energy delivery to the hive, whereas those in large colonies may seek instead to maximize efficiency, since small colonies will probably benefit more from a high short-term growth rate (Houston et al. 1988). Precisely this pattern has been reported for bees studied in *late* summer (Fewell et al. 1991), though not for those studied in *mid*-summer (Wolf and Schmid-Hempel 1990; Eckert 1990). These findings are consistent with those reported in the present paper, namely that bees from a small colony in *mid*-summer were apparently trying to maximize the efficiency, rather than the rate, of their foraging. Perhaps nectar foraging honey bees usually operate with a goal of maximizing energetic efficiency but will switch to one of maximizing rate of energy acquisition whenever their colony's energy situation becomes extremely bad, i.e., winter is near and the colony has low population or low food stores, or both.

Further considerations of functional design

This study has described various features of the way a forager bee transduces the stimulus of nectar-source profitability into a waggle-dance response. These include the shape of the stimulus-response function, the rate of adaptation in the dance response, and the tuning of the dance response threshold. Presumably, these features are not arbitrary, but instead are the result of natural selection for behavioral traits that enhance reporting of information about food sources. To understand the functional design of these traits, it is useful to draw a comparison for each trait between a forager bee and a sensory neuron (Table 3). To be sure, there are profound differences between these two forms of sensory units, including the

Table 3. A comparison of sensory neurons and honey bees as sensory units

Feature of sensory unit	Primary sensory neuron	Forager honey bee
Transduction	Often unidimensional, by one or a few cells	Multidimensional, by a multicellular organism
Stimulus coding	Frequency of spikes (a time-dependent output), no amplitude modulation	Duration of waggle run series (a time-dependent output), no amplitude modulation
Stimulus range (suprathreshold)	Broad, up to several (8+) orders of magnitude	Narrow, one order of magnitude
Response range	1-1000 spikes/s	1-100 waggle runs/dance
Stimulus-response ratio	Often much greater than 1, and up to 100000 or more	Less than 1
Stimulus-response function	Logarithmic or power	Linear
Adaptation rate	Low to high (tonic to phasic response)	Low, if not zero (tonic response)
Inter-unit variation in response threshold	Common	Pronounced
Adaptive tuning of response threshold	Dynamic range shifts	Dynamic range expands and contracts
Spatial arrangement of output	Often preserves information about the external environment (somatotopy, tonotopy, etc.)	Little or no preservation of external spatial information

fact that a bee is a multicellular unit able to provide a complex, multidimensional report (food-source direction, distance, odor, and profitability) whereas a sensory neuron is a unicellular unit that often provides only a simple, unidimensional report (such as illumination intensity or temperature). At the same time, however, there are fundamental similarities between the two, such as the fact that both use a time-dependent output (duration of waggle run series vs. frequency of spikes) and that neither uses amplitude modulation of the pulses in the signal (waggle runs and spikes) to code stimulus intensity. By noting the similarities and differences between these two forms of information acquisition devices, perhaps we can better understand the functional design of each.

Consider first the general form of the stimulus-response relation. For bees we have seen that for supra-threshold stimuli (X), the response (Y) is a linear function of the stimulus ($Y = a \cdot X + b$), whereas for many sensory neurons it is best described by a logarithmic function ($Y = \log_a X$, Weber-Fechner law) or a power function ($Y = a \cdot X^b$, Stevens law), usually with $b < 1.0$ (Somjen 1972). Why is there this difference? I suggest that the answer lies in the marked difference between the two cases in the ratio of stimulus range to response range. For many sensory cells, such as sound and light receptors, the detectable stimuli can vary in intensity by a factor of 10^8 or more. At the same time, these cells can vary their response only by a factor of about 10^3 , that is from about 1 spike/sec (the minimum frequency that is distinguishable from background firing) to about 1000 spikes/sec (the maximum firing frequency, set by the action potential duration and its recovery processes) (Mellon 1968). Clearly, for a single cell to report on stimuli over such a broad range of intensities and simultaneously resolve low-level stimuli, its output will have to be a logarithmic (or exponential) function of the input. Turning to bees reporting on nectar-source quality, we find a completely different situation. As we have seen (Table 2), the stimuli that the bees report on vary in intensity by only a factor of about 10, whereas the bees can vary their dance response by a factor of about 100. Obviously bees do not need to make their output a logarithmic function of input to be able to cover the full range of inputs and maintain good resolution of low-level stimuli. A simple linear function will do.

Now consider the rate of sensory adaptation. Neurons vary greatly in this design parameter, with some (phasic receptors) adapting quickly and others (tonic receptors) adapting slowly or not at all. It is well known that these distinct adaptation patterns serve two different sensory needs of an organism. A phasic receptor provides information about the *changes* in a stimulus while a tonic receptor keeps an animal informed about the *level* of a stimulus (Young 1989). These ideas seem to also explain the adaptation rate of the dance response. A dancing bee should report to her nestmates the level of profitability of her nectar source, rather than the changes in its profitability, since it is the actual level of profitability (not how much the profitability has changed) that ultimately determines the attractiveness

of a nectar source.³ For example, if a flower patch provides rich foraging throughout a day, then all else being equal, the foragers from this patch should perform a long recruitment dance every time they return to the hive. Hence from the perspective of functional design it makes good sense that the dance response of bees shows exceedingly slow (or even no) adaptation.

Tremendous variation in response thresholds is a striking trait of both dancing bees (Fig. 1 and Table 2) and of sensory neurons of virtually all modalities (Young 1989). The principal effect of this variation is that it increases the ability of the total sensory system (i.e., the complete set of sensory units) to show a graded response across a broad range of stimuli. In contrast, if there was no variation among sensory units in response threshold then the dynamic range (i.e., the range of stimuli over which there is a graded response) of the total sensory system would be only as wide as the dynamic range of a single unit. In the case of the bees, it is possible that this variation among individuals in dance threshold is partly a result of the genetic variation among individuals, which is in part a consequence of multiple mating by the queen (reviewed by Page and Robinson 1991). Thus this demonstration of inter-individual variation in the dance threshold is consistent with the idea that a honey bee queen mates multiply in order to improve her colony's ability to cope with a wide range of environmental conditions (Crozier and Page 1985). To test this hypothesis, we need to determine whether the variation among individuals in dance thresholds is indeed a product of genetic variation among individuals, and whether colonies with low and high genetic variation differ substantially in the range of food sources over which they can produce a graded recruitment response.

As for tuning of the response threshold, this is now well documented for dancing bees (Fig. 3), as well as for various sensory neurons, such as the retinula cells of insect eyes (Laughlin and Hardie 1978). For sensory cells, the typical situation is for the response threshold to be shifted to match the level of background stimulation, thereby enabling the cell to keep its dynamic range matched to the range of stimulus intensities it experiences at any given time. This also enables a cell with a limited dynamic range to operate over a wider range of intensities than it would otherwise. For a dancing

³ A recent study (Raveret Richter and Waddington 1993) suggests, however, that when bees assess the attractiveness of a nectar source, they consider not only its current profitability, but also whether its profitability has recently risen or fallen. They found that honey bees performing round dances vary certain parameters of this dance (rate of direction reversal, circuit rate, and speed) in relation to their past experience at a sugar solution feeder, not just their immediate experience there. In particular, for any given concentration of sugar solution at the feeder, foragers performed livelier round dances if the feeder had recently offered a lower concentration than if it had offered a higher concentration. It will be important to determine whether the observed differences in round dance liveliness result in changes in the recruitment effectiveness of these round dances. It will also be important to test whether or not bees performing *waggle* dances vary the number of waggle runs per dance in relation to recent changes in a food source's profitability, not just its current level of profitability

bee, the functional significance of changing the response threshold is probably quite different from that of a sensory neuron. In particular, it probably functions as a mechanism for minimizing the probability of colony starvation when food is sparse ("risk avoidance"; Stephens and Krebs 1986) and maximizing the efficiency of foraging when food is abundant. Previous studies (Lindauer 1948; Seeley 1986) have shown that bees lower the dance threshold when food becomes sparse, and this is the pattern observed in this study as well (Fig. 3). During the nectar flow, only a highly profitable feeder (2.0 mol/l) elicited recruitment dances, but then a week or so later, after the nectar flow, even a moderately profitable feeder (1.0 mol/l) caused the bees to dance. By lowering their response threshold when food becomes sparse, bees increase the quality range of exploited food sources and so decrease their colony's probability of starvation. By raising this threshold when food becomes abundant, the bees filter out low-yield sources when they are not needed and so increase their colony's foraging efficiency.

Finally, there is the matter of the spatial organization of sensory input. For neurons it is often the case that the spatial arrangement of their output preserves information about the outer world. For example, touch receptors in most vertebrates are somatotopic, that is, the sensory fibers for touch terminate in the thalamus in an orderly geometrical arrangement that preserves the relations of the body surface (Shepherd 1988). No doubt this topographical representation of tactile information facilitates the higher-order processing by keeping functionally related sensory information together and unrelated information apart. In the case of dancing bees, we see just the opposite arrangement, with dances for topographically distinct forage sites performed in a mosaic pattern on the dance floor (Fig. 5). Hence dances are performed in a geometrical arrangement that erases most, though not all (see also Fig. 22 in Boch 1956), of the information about the spatial relations of the forage sites. (Note: the slight spatial separation of dances for different sites is evidently just a by-product of the tendency of dancing bees to drift across the dance floor in the direction of their waggle runs, as shown in Fig. 4. Such drift within individual dances, however, may itself be adaptive since it helps broadcast each bee's recruitment signal.) I suggest that the adaptive significance of the absence of strong spatial segregation of dances for different forage sites is that this helps the bees who are following dances to sample randomly among them. By having the dance-producing bees intermingle the dances for different sites, and by having the dance-following bees follow just one dance before leaving the hive to search for a new food source, the foragers of a colony distribute themselves among the forage sites reported in the hive approximately in proportion to their quality (Seeley and Towne 1992). It is now known that this distribution of foragers among sites (approximately an "ideal free distribution", Fretwell and Lucas 1970) results in highly efficient extraction of resources from the environment (Bartholdi et al. 1993).

Conclusions

A honey bee colony achieves its reconnaissance about food sources by having its foragers function as sensory units, with each bee transducing its experiences at a forage site into a dance that transmits information about the location and profitability of the site. This generates an ever-changing display inside the hive of information about the foraging opportunities outside the hive. Novice or unsuccessful foragers can refer to this information display for guidance about the locations of profitable forage sites. Clearly, this system depends upon each forager being able to properly report on her foraging experience. We see that foragers are evidently well adapted to this task. Specifically, it appears that many details of the dance response of bees – including the linear coding of forage-site quality, the low rate of dance adaptation, the strong tuning of the dance threshold, and the dispersed presentation of dance information – represent adaptations to enhance a bee's effectiveness as a sensory unit reporting on the world outside the hive.

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