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Honey Bee Communication: The Dance-Language Controversy

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H O N E Y B E E C O M M U N I C A T I O N :
T H E D A N C E - L A N G U A G E C O N T R O V E R S Y

A Thesis submitted to the Faculty of The Rockefeller University
in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

by

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The Rockefeller University
New York

PREFACE

My interest in animal behavior began with Dr. Seymour Benzer's course in behavioral biology at Caltech. His enthusiasm and encouragement led me to abandon bacteriophage for honey bees. His interest in the dance-language controversy first drew my attention to what is the central problem for this thesis: whether honey bee recruitment involves an abstract language. Dr. Donald R. Griffin's interest in the same question has helped to sustain and guide this effort. Dr. Peter Marler, Dr. Fernando Nottebohm, and Dr. Roger Payne have each, in their own way, helped me gain a proper ethological perspective. The members of my thesis committee--Dr. Marler, Dr. Keffer Hartline, Dr. Bert Hölldobler, and in particular, Dr. Griffin--provided valuable advice and criticism. At each stage in the progress of this study, Dr. Norman Gary has provided valuable advice and encouragement. Mike Rossetto designed the electronic devices which proved essential for collecting my data. Dr. Robert O'Connell obtained the scents used here as a gift from International Flavors and Fragrances, Inc., and suggested using curare on honey bees. Dr. E. O. Wilson suggested somehow using a live bee as a model. To each of these gentlemen I offer my sincere thanks.

The plan of this thesis is to describe briefly the natural history of the honey bee, and then to trace the development of the dance-language controversy. Next, my recent efforts to develop an unambiguous approach and the results of eighteen experiments will be described. I hope that these experiments will cast some light on earlier work which has recently been criticized, and will add to the understanding of honey bee recruitment. Finally, some of the more general questions raised by the honey bee language and controversy will be considered.

SUMMARY

In recent years, the evidence suggesting that honey bees communicate with a "dance language" has been strongly attacked on both theoretical and experimental grounds. The controversy is reviewed and the main issues are isolated and discussed. The fundamental obstacle to the resolution of this important dispute has been that dancing bees advertise a food location with specific odor information as well as with symbolic distance and direction coordinates. Since recruited bees seem able to find food on the basis of site-specific locale odors alone, a conclusive test would be one in which the dancer gave symbolic directions to a location to which it had never been. If recruits do not use the language, they would show no preference for the station indicated by the dance.

In theory there are at least three ways to perform an unambiguous experiment. One way is to use a dummy bee whose dance parameters are directly controlled by the experimenter. Progress along this line is described. A second way would be to cause the foragers to "lie" about distance. The theoretical and practical difficulties associated with this approach are discussed. Finally, foragers could be caused to lie about direction. A practical technique to accomplish this misdirection of dance information is described. The ocelli of forager bees are covered with paint, making the bees six times less sensitive to light. In the hive, an artificial sun is used to reorient bees. Since the ocelli-painted foragers do not respond to the light, they orient their dances with respect to gravity, while untreated bees interpret the dances with respect to light. Hence, if recruits use the abstract distance and direction information in the dance, they would be expected to fly to a specific but incorrect location in the field. In fact, recruits do precisely that, proving unambiguously that the symbolic dance communication is a real phenomenon.

Since the misdirection technique removes the many odor problems associated with previous work, more precise measurements of distance and direction accuracy are possible. Recruit accuracy was measured, and theoretical problems inherent in the interpretation of such results are discussed. The notion that bees must integrate separate dances was tested

and found unlikely. The effects of the techniques of von Frisch and Wenner were also examined. Von Frisch's methods increase the observed accuracy moderately, while Wenner's decrease it dramatically. A technique for automatically capturing and counting recruits is also described.

The questions of in what sense honey bees may be said to possess a language or to be "rational" are also considered. A reformulation of the dance-language hypothesis is presented.

TABLE OF CONTENTS

PREFACE	ii
SUMMARY	iii
THE LIFE OF THE BEE	1
The Swarm.	1
The Worker	2
The Drones	2
The Queen.	3
RECRUITMENT	4
Early Theories of Honey Bee Recruitment.	4
The Olfaction Theory	4
Failure of the Olfaction Theory.	6
The Dance Language	8
Honey Bee Orientation.	11
Details of the Dance	13
Recruitment without Dancing.	15
Accuracy of the Dance.	16
How Unique are Honey Bees?	18
Are von Frisch's Experiments Conclusive?	22
THE DANCE-LANGUAGE CONTROVERSY.	23
Wenner's Attack.	23
Von Frisch Replies	29
Wenner and Johnson Reply	34
Another Exchange	35
ATTEMPTS TO RESOLVE THE DANCE-LANGUAGE CONTROVERSY.	36
Attempts to Control for Cues Left in the Field	36
Gould, et al. Series I.	37
Gould, et al. Series II	39
Further Studies of the Behavior of Individual Recruits	43
Esch and Bastian's Experiments.	43
Mautz's Experiments	44
Further Attempts to Control for Cues Left in the Field	44
THE DEVELOPMENT OF ALTERNATIVE THEORIES OF RECRUITMENT.	46
The Olfaction Theory	46
Which Odor Cues are Important?	47

Do Bees Integrate Dances?	48
The Importance of Locale Odor	49
The Locale Odor Theory.	50
The Odor-Trail Hypothesis	51
AN OBJECTIVE TEST OF THE DANCE-LANGUAGE THEORY	53
Causing Foragers to Lie About Distance.	53
THE MODEL BEE.	57
Previous Attempts	57
Reproducing the Shape and Waggle of the Dance	58
Reproducing the Smells and Tastes of the Dance.	61
Reproducing the Dance Sound	62
Hearing through the Legs	62
Hearing with the Antennae.	65
CAUSING FORAGERS TO LIE ABOUT DIRECTION.	70
PROTOCOL	72
Training.	72
The Artificial Sun.	78
Recording the Dancing	80
The Artificial Flowers.	83
The Locale.	85
The Weather	85
Time of Day	85
DIRECTION COMMUNICATION AND ACCURACY	85
150 m Arrays.	85
400 m Arrays.	90
Accuracy.	101
Effects of the von Frisch Techniques.	105
Effects of Wenner's Techniques.	106
DISTANCE COMMUNICATION AND ACCURACY.	118
Short-Distance Experiments.	118
Longer-Distance Experiments	126
Distance Accuracy	126
Effects of von Frisch Techniques.	126
Effects of Wenner Techniques.	138
INTEGRATION OF SEPARATE DANCES	145

SOME IMPLICATIONS OF THE DATA	150
Do Recruits Arrive in Groups?	150
How Long Do Recruits Take?	159
Theoretical Limits to the Accuracy of Recruitment.	163
How Do Recruits Reach the Food?	164
The Training Issue	168
THE DANCE-LANGUAGE CONTROVERSY IN RETROSPECT.	169
Teleology and the Dance-Language Controversy	169
Was the Controversy a "Revolution"?	170
The Dance-Language Hypothesis: A Reformulation	177
THE DANCE LANGUAGE AS A "LANGUAGE".	179
The Information Content of the Dance	179
Do Honey Bees Have a Language?	183
Are Honey Bees "Rational"?	187
BIBLIOGRAPHY.	195

LIST OF FIGURES

1	The Round Dance	5
2	An Early von Frisch Experiment.	7
3	Transition from Round to Waggle Dance	9
4	The Waggle Dance.	10
5	Distance Correlation in the Dances of Italian Honey Bees. . . .	12
6	A von Frisch "Fan" Experiment	17
7	Results of the Fan Experiments.	19
8	A von Frisch "Step" Array	20
9	Results of the Step Experiments	21
10	Johnson's Fan Array	24
11	Wenner's Step Array	27
12	Von Frisch's Horizontal/Vertical Hive Experiment.	31
13	Array of Gould, et al.	38
14	Results of Series I	40
15	Lindauer/Wenner, et al. Array	45
16	Dances of Walking Italian Foragers.	54
17	The Gonçalves Array	56
18	Model Bee Device.	59-60
19	Response of the Subgenual Organ	63
20	The Head of the Honey Bee	67
21	Resonances of the Antenna	68
22	Minimum Light Levels for Forager Flight	71
23	Minimum Light Levels for Phototaxis	73
24	Dance Reorientation to an Artificial Sun.	74
25	A Recruit Station	75-76
26	The Artificial Sun.	79
27	Distribution of Dancing on the Comb	81
28	Parallax Error for Dance Attenders.	82
29	The Experimental Field.	86
30	Topographic Map of the Field.	87
31	150 m Direction Array	88-89
32	Recruit Distribution in Experiment 2 (150 m Direction Array). .	91
33	Recruit Distribution in Experiment 4 (150 m Direction Array). .	93
34	400 m Direction Array	95-96

35	Recruit Distribution in Experiment 7 (400 m Direction Array). . . .	97
36	Recruit Distribution in Experiment 8 (400 m Direction Array). . . .	99
37	Recruit Direction Accuracy.	102
38	Dance Following Strategy.	103
39	Residual Misdirection	104
40	Von Frisch Direction Control I Array.	107-108
41	Recruit Distribution in Experiments 9 and 19 (von Frisch Controls). . . .	109
42	Von Frisch Direction Control II Array	111-112
43	Recruit Distribution in Experiment 15 (Wenner Direction Control). . .	114
44	Recruit Distribution in Experiment 16 (Wenner Direction Control). . .	116
45	Closer Distance Array	119-120
46	Recruit Distribution in Experiment 1 (Closer Distance Array). . . .	121-122
47	Recruit Distribution in Experiment 3 (Closer Distance Array). . . .	124
48	Farther Distance Array.	127
49	Recruit Distribution in Experiment 5 (Farther Distance Array) . . .	128
50	Recruit Distribution in Experiment 6 (Farther Distance Array) . . .	130
51	Recruit Distance Accuracy	132-133
52	Von Frisch Distance Control I Array	134-135
53	Recruit Distribution in Experiment 11 (von Frisch Control).	136
54	Von Frisch Distance Control II Array.	139-140
55	Recruit Distribution in Experiment 12 (von Frisch Control).	141
56	Recruit Distribution in Experiment 16 (Wenner Distance Control) . .	143
57	Array for Wenner, et al. Control.	146-147
58	Recruit Distribution in Experiment 17 (Wenner, et al. Control). . .	148
59	Array for Lindauer "Integration" Control.	151-152
60	Recruit Distribution in Experiment 13 (Lindauer Control).	153
61	Recruit Distribution in Experiment 14 (Lindauer Control).	155
62	Recruit Distribution in Integration Experiments	157-158
63	Recruit Arrival Intervals	160
64	Recruit Search Times.	161
65	Olfactory Homing Strategy	166-167

LIST OF TABLES

I	Results of Johnson Direction Experiment.	25
II	Results of Wenner Distance Experiment.	28
III	Results of Gould, et al. Series II	42
IV	Results of Experiment 2 (150 m Direction).	92
V	Results of Experiment 4 (150 m Direction).	94
VI	Results of Experiment 7 (400 m Direction).	98
VII	Results of Experiment 8 (400 m Direction).	100
VIII	Results of Experiment 9 (von Frisch Direction Control) . .	110
IX	Results of Experiment 10 (von Frisch Direction Control). .	113
X	Results of Experiment 15 (Wenner Direction Control). . . .	115
XI	Results of Experiment 16 (Wenner Direction Control). . . .	117
XII	Results of Experiment 1 (Closer Distance).	123
XIII	Results of Experiment 3 (Closer Distance).	125
XIV	Results of Experiment 5 (Farther Distance)	129
XV	Results of Experiment 6 (Farther Distance)	131
XVI	Results of Experiment 11 (von Frisch Distance Control) . .	137
XVII	Results of Experiment 12 (von Frisch Distance Control) . .	142
XVIII	Results of Experiment 18 (Wenner Distance Control)	144
XIX	Results of Experiment 17 (Wenner, et al. Control).	149
XX	Results of Experiment 13 (Lindauer Control).	154
XXI	Results of Experiment 14 (Lindauer Control).	156

THE LIFE OF THE BEE

Honey bees make their living from flowers. Many plants need insects to transfer pollen from one flower to another, thereby avoiding inbreeding. The insects are rewarded for this service with nectar, which they need as a carbohydrate source. The nectar is treated with enzymes -- invertases -- to change the sugars into forms which are less useful to bacteria and yeast. It is then thickened by evaporation into honey. Unlike wasps, bees use pollen rather than insect prey as a protein source.

This thesis deals primarily with the ways in which honey bees orient themselves and recruit each other to food sources. The social organization of honey bees, however, is equally fascinating, and intimately connected to recruitment. A fuller account may be found in Ribbands (1953), Butler (1963), Wilson (1971), Michener (1974), and Gary (1974).

The Swarm

In the spring, as the population of a honey bee colony increases to as many as 100,000 individuals, the hive "reproduces" by swarming. About half of the bees fly out with the queen and form a cluster on a nearby branch. Several days later, the swarm flies to a vacant cavity and starts a new colony.

Their first step is building comb. Honey bee comb is constructed from beeswax, a substance secreted by special glands in the abdomen. The scales of wax are worked into large sheets of hexagonal cells. These cells serve to store food -- nectar, pollen, and honey -- as well as to raise new bees.

Once cells are available, the queen begins laying eggs -- up to 3000 per day. The eggs hatch into larvae after three days. If the queen has fertilized an egg with some of her stored sperm, it will develop into either a worker or another queen, depending on the diet fed to the larva. If the egg has not been fertilized, it develops into a haploid drone. The larvae are first fed a substance -- royal jelly -- secreted by "nurse"

worker bees. Unless the larva is being raised as a queen -- something which is done only when the queen is failing or the hive is preparing to swarm -- this diet is slowly replaced by a mixture of pollen and honey. After about a week, the larvae are sealed into their cells with wax, where they pupate. When the new bee is ready to emerge several days later, it cuts away the capping and struggles out of the cell.

The Worker

Although the life cycle of worker bees depends on the needs of their hive, a very general picture can be drawn. Workers begin their brief lives by cleaning the hive. Soon, however, their "nurse" glands develop, and they spend several days feeding larvae and the queen. Later, these glands atrophy, and the wax glands begin to function. The worker can then secrete wax and build comb. When these glands atrophy in their turn, the bee may begin guarding the hive, unloading incoming foragers, and taking occasional "play flights." As guards, they detect intruders which lack the hive's unique odor. Intruders are expelled, or killed if necessary. At night, bees may be found fanning cells of nectar, causing the contents to thicken into honey. Finally, three weeks after hatching, a worker may begin foraging for food. After another three weeks, the forager will "wear out" and die.

The Drones

Although Aristotle thought that drones must be female, since they had no stings, they are males. Drones are produced primarily in the spring, and are thrown out in the fall when sources of nectar and pollen begin to fail. Since drones cannot feed themselves, this expulsion is fatal. Under natural circumstances, vast numbers of drones are produced. Commercial techniques keep the drone population much lower. Drones fly out each afternoon to traditional congregation areas. There, the drones from many colonies fly about awaiting the rare arrivals of unmated queens. Since no drones live through the winter, and yet the congregation areas remain constant from one year to the next, some permanent feature of the area must be involved.

When a queen arrives at a congregation area, a vast "comet" of drones pursues her in an attempt to mate. The successful drone is rewarded by an instantaneous death. After two hours or so in the congregation, drones return to their respective hives.

The Queen

Aristotle considered the queen to be a king, but nevertheless knew that she was usually necessary to produce workers. Since he had no observation hive, he had no way of knowing who laid the eggs -- although he did discount the theories that the eggs were gathered from flowers. The occasional worker which can lay drone eggs obscured the normal picture.

When a new queen is preparing to emerge, she produces a pulsed sound which causes the bees in the hive to "freeze." The sound travels through the wax combs and is detected by the subgenual organs of the legs. Freezing the workers probably quiets ever larger portions of the hive until the old queen can detect the signal. The old queen "answers" by pressing her thorax against the comb and signalling back. The messages may be "I am ready to emerge, so you may leave with the swarm," and "I am still here, so stay where you are." This would be an important message, since the time of day or weather may not permit swarming for some time. Queens do not usually tolerate each other in the same hive.

Once the swarm is gone, the new queen emerges and kills any unemerged queens. Since the first to emerge passes on her genes, it is hardly surprising that queens pass through the pupal stage in only 4 days, rather than the 7 and 10 required for workers and drones.

The new queen will produce pheromones throughout her life which attract workers to her and "calm" the hive. When she flies out to the congregation area, however, these same pheromones will induce drones to mate with her. Why drones in the hive are unaffected by these odors is not known. Queens mate with several drones, and then begin to lay. Although they can still fly -- as they must to accompany swarms in succeeding years -- when they run out of stored sperm, the queens do not attempt to leave and mate again; they are simply replaced.

When the winter comes, the queen ceases laying, and the colony clusters in a clump and attempts to maintain a temperature of 34-36°C from the heat generated by "shivering," utilizing the insulation of thousands of bees. The same temperature is maintained during the rest of the year as well, even though in the summer the workers may have to air condition the hive by evaporative cooling.

If the stores of honey last through the winter, the colony may survive. As the spring comes and food becomes plentiful, the queen begins laying again, and the population increases sharply. If the hive becomes crowded or too large, the colony may swarm.

RECRUITMENT

Early Theories of Honey Bee Recruitment

More than 2000 years ago, Aristotle noticed that when a dish of honey is set out near a hive, it may take hours or even days for a forager honey bee to find it. Once the food is discovered by even a single bee, however, new bees soon begin to arrive. The forager must, in some way, have "recruited" these new bees. Aristotle thought that the recruit bees simply followed the forager to the food.

Maeterlinck (1901) tested this explanation by letting a forager find the food and return to the hive. He then caught the forager on its way back out of the hive. Even though recruited bees had no forager to follow, some of them nevertheless found the food. A forager must communicate to recruits enough information for them to find the food by themselves. Maeterlinck speculated that some "tactile language or magnetic intuition" might be involved.

The Olfaction Theory

By 1923, von Frisch had completed a series of careful investigations to discover just what information is communicated from forager to recruit. As had others before him, von Frisch noticed that the returning forager often (but not always) performs a "dance" (Fig. 1) which attracts the attention of other bees in the hive. The bees "attending" the dance run after

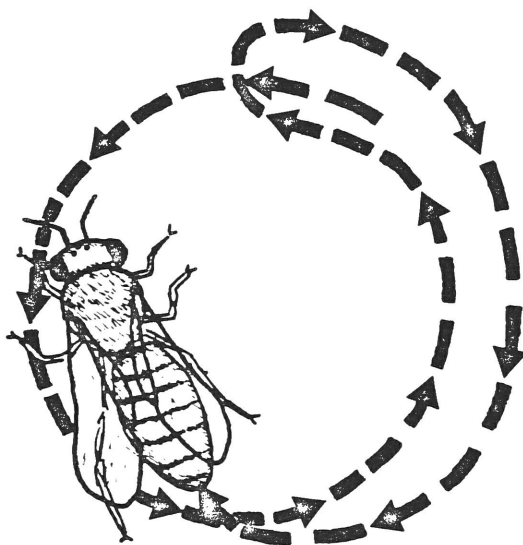


Fig. 1. The Round Dance. The returning forager runs in circles, reversing direction at about $1\frac{1}{4}$ sec. intervals. The dance is most commonly performed in the darkness of the hive on the face of one of the vertical combs. Interested bees attend the dances, running after the forager in an apparent attempt to maintain antennal contact. Occasionally the dancer may stop and offer samples of nectar to the attenders. Many of the attenders subsequently leave the hive, and some may later locate the food. Besides nectar, the round dance may be used to signal the discovery of water, pollen, propolis, or even new nest sites. Dances are usually performed when the item discovered is in short supply -- not the usual situation. Under more normal circumstances, dancing may be quite rare. Redrawn from von Frisch 1967a, p. 28.

and maintain antennal contact with the dancer's body. Occasionally, the dancer stops and regurgitates samples of the food which the attenders taste. By giving the recruited bees a choice of foods, von Frisch (1919) showed that recruits know the odors present at the food source being visited by the forager.

The odor could be in the food, and hence be available in the regurgitated sample; or the odor could simply be in the vicinity. For example, if the food dish is placed on a wire mesh, and the odor is placed on a piece of filter paper below the mesh, feeding foragers never come into direct contact with the odor. Nevertheless, recruits are able to select the correct odor from an array of odors. Von Frisch (1923) demonstrated that the waxy hairs of bees absorb odors (see also Steinhoff 1948). When a forager dances in the hive, the appropriate odors are present on its body. Since, as von Frisch (1921) also showed, bees have olfactory receptors on their antennae, the dance attenders must learn the odor by examining the forager's body with their antennae.

In summary, the "olfaction theory" explained recruitment on the basis of food-source odors brought back to the hive in and on the body of the forager. The dances serve to attract the attention of potential recruits, to provide them with an opportunity to learn the food-source odors, and to give them a sample of the food which is available there.

Failure of the Olfaction Theory

In the early 1940's, von Firsch (1947) realized that recruit bees seem to know the general location of the food source being visited, especially when the source is some distance away. In a specific example (Fig. 2), although all feeding stations contained the same food, recruits landed only in the general area of the station being visited by the foragers. There are at least three classes of additional information, not mutually exclusive, which might be available to the recruit to help it locate the food source.

First, the forager might leave cues at and near the food source. Honey bees have a scent gland on the abdomen which can release an "assembly"

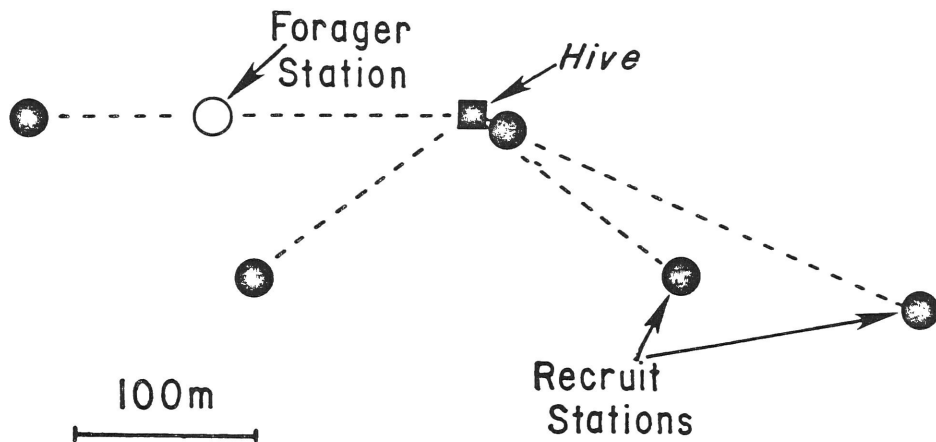


Fig. 2. An early von Frisch experiment. A group of foragers was trained to the station indicated. A weak, unscented sugar solution was used during training so that no dancing occurred and no recruitment was elicited. During the experiment the foragers were fed a concentrated, anise-scented solution which released vigorous dancing. Pieces of filter paper soaked with anise scent were set out at various locations ("Recruit Stations"). Recruits searching on the basis of food odor alone would be expected to arrive at all stations. In reality, however, 115 recruits arrived at the Forager Station, 173 recruits at the two nearest Recruit Stations, but only 32 recruits at the remaining three stations. Recruits clearly favored the area being visited by returning foragers. The wind speed and direction were not stated. Redrawn from von Frisch 1947.

pheromone (von Frisch 1923). A forager at a rich source of food often exposes and fans this gland, especially when the natural scent is weak (Free and Williams 1970). The pheromone, a mixture of citral and geraniol (Boch and Shearer 1962, 1964; Butler and Calam 1969), attracts other bees to the area. By exposing its scent gland, a forager could "mark" an area. In addition, each colony has a unique "hive odor" which its members "exude" wherever they are. This odor attracts other bees from the same hive (von Frisch and Rösch 1926; Kalmus and Ribbands 1952; Ribbands, Kalmus and Nixon 1952; Ribbands 1955; Renner 1960), and could also serve to mark an area. Finally, the mere sight of other bees attracts recruits (Kalmus 1954; Wenner et al. 1969), and serves as still another cue which might be specific to the area of the food source.

A second possibility is that foragers might bring back odors unique to the area of the food source. Various locales -- a marsh, a rocky field, a pine woods, the edge of a pond -- have their own unique odors which can be absorbed by the forager's body and sensed by recruits. Even recruits which have never foraged have nevertheless undertaken extensive "play flights" (Ribbonands 1953), and hence had an opportunity to learn the olfactory landscape. Recruits should be able to at least approximately "place" a food source from the locale odor on the forager. Bees are clearly able to associate odors with locations (Ribbonands 1954; von Frisch 1967a, pp. 23, 30-35, 67, 152-153).

A third possibility is that honey bees have some sort of abstract, symbolic communication -- a "language" or "secret sign" (1924, cited in von Frisch 1947) -- by which the location of a food source is communicated from forager to recruit.

The Dance Language

Alerted to the problem, von Frisch later discovered that the round dance (Fig. 1) is performed when the food source is near the hive, while a second dance form begins to appear as the source is moved to greater distances (Fig. 3). This second type, the "waggle dance," consists of a straight run during which the forager vibrates or waggles its body from side to side, alternated with a hurried semicircular return to the starting point (Fig. 4). The tempo of the dance -- the number of waggle runs



Fig. 3. Transition from Round to Waggle Dance. As the foragers have to fly further to a food source, the round dance (left) slowly becomes the waggle dance (right). The duration of the waggle runs increases with distance; and while the average orientation of the runs remains constant, the extreme alternation of succeeding runs to the right and left of average decreases with distance. For Italian bees (Apis mellifera ligustica) the round dance is performed for sources up to 20 m from the hive, while at 100 m the dance form second from the right is most common. Redrawn from von Frisch 1967a, p. 61.

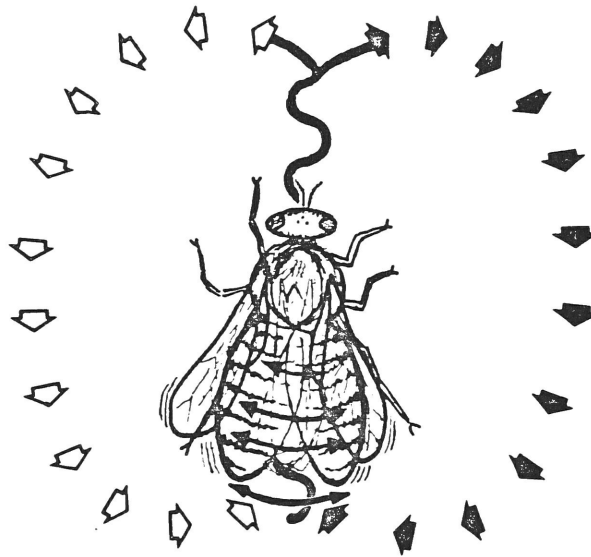


Fig. 4. The Waggle Dance. The returning forager runs in short straight lines, vibrating its body from side to side as indicated. The straight runs are followed by a rapid semicircular return to the starting point. Returns usually alternate to the left and right. The duration of the straight runs increases with distance at the rate of about one complete waggle per 25 m. The orientation of the straight runs with respect to vertical (i.e., gravity) reflects the direction of the food with respect to the sun. Although normally performed in the dark on the vertical comb in the hive, foragers can dance in view of the sky. In these cases the dances are oriented with respect to the sun, while the distance correlation is unaffected. Redrawn from von Frisch 1967a, p. 57.

per minute -- decreases as a feeding station is moved further away (Fig. 5), thereby reflecting the distance to the food.

When the dancing bees are prevented from seeing the sky (the usual situation in a natural hive), another correlation emerges. The direction of the food relative to the sun is the same as the direction of the waggle run with respect to gravity. Von Frisch concluded that the distance and direction information in the dance is communicated to and used by recruited bees (von Frisch 1947).

Honey Bee Orientation

The renewed interest in honey bees soon brought many more remarkable discoveries. The more primitive species of honey bees live in tropical areas and build their colonies in the open, dancing in full view of sun and sky (Lindauer 1961). Honey bees can perform oriented dances even when the sun is not visible. Von Frisch (1949) showed that the dancers can infer the sun's location from patterns of polarization in the blue sky (or even through a thin cloud cover [see also Zolotov and Frantsevich 1973]).

The insistence of our honey bee, Apis mellifera, on living in enclosed hives is the behavioral adaptation which permits them to overwinter in temperate areas (Wilson 1971). Even our enclosed-hive honey bees still orient their dances directly to the sun when it is visible (during swarming, for example).

Since the sun appears to move from east to west at about 15° per hour, the direction of a food source with respect to the sun changes at the same rate. Bees learn to compensate for this movement, and correct their dance orientations accordingly (von Frisch 1947). (Departures from the 15° per hour average are extreme during that part of the year when the sun passes near the zenith. Whether bees can compensate accurately under these circumstances without frequent glimpses of the sun is unclear.)

Many flowers produce nectar only at particular times of day. Foragers learn to visit these sources at the correct times, and have been proven capable of remembering many separate sources at different times of day (Beling 1929). Honey bees can remember a location for at least 173 days (Lindauer 1963).

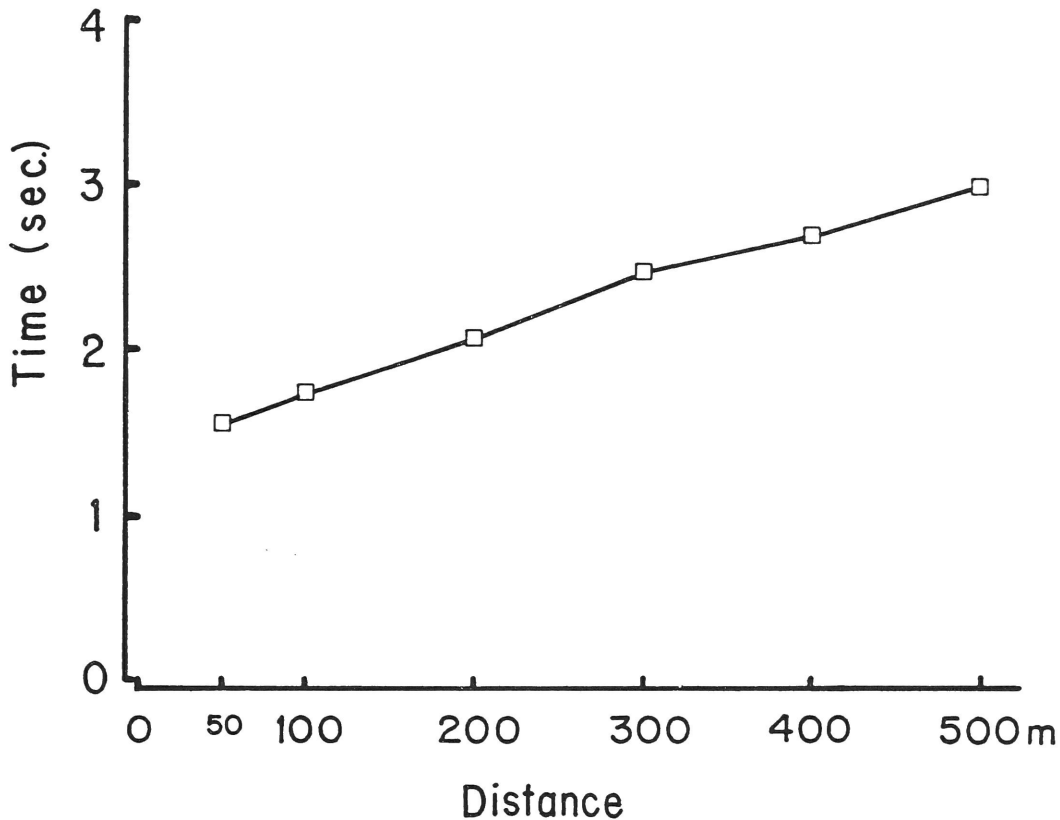


Fig. 5. Distance Correlation in the Dances of Italian Honey Bees. As the food source is moved farther away, the duration of each dance cycle increases. The duration of the waggle phase of the dance accounts almost entirely for the increase, each additional wag corresponding to about 25m and adding approximately $1/13$ sec. to the total time. Although not shown here, the curve continues with approximately the same slope to beyond 10 km. The curve is plotted from data gathered during the summer of 1974, and represents the average of 250 dances of at least 6 cycles at each distance. (The distance correlation curve is often described as logarithmic, a result of von Frisch's preference for measuring the number of dance cycles per 15 sec.)

After locating a new source, a forager must calculate the direction from the hive to the food. Although the dance reflects this calculation, the forager need not have flown in the direction being indicated -- bees can integrate the separate legs of an indirect route (von Frisch 1948; Lindauer 1963). Similarly, although a forager must alter its orientation when flying in a crosswind, it nevertheless signals the map direction of the source (von Frisch and Lindauer 1955).

If there are landmarks along the route, foragers will use them for navigation. For example, von Frisch and Lindauer (1954) put a hive along the edge of a north-south line of trees. They trained their foragers along the trees to the north. During the night, the hive was moved to the edge of an east-west line of trees, and stations were put out to the east, west, and north. The foragers ignored the sun and flew along the trees to the west. (It would be interesting to know whether the foragers' dances signalled the direction flown on the previous day. Unfortunately, there is no record of the direction signalled by these foragers when they returned to the hive and danced.)

Bees have also been shown to be able to orient to magnetic fields. There is a slight error in the transposition from light to gravity in the dance, but it disappears when the earth's magnetic field is artificially eliminated (Lindauer and Martin 1968). Comb in new hives is oriented in the same direction as in the parent hives. The bees use the earth's magnetic field to determine the proper orientation (Lindauer 1973, 1974; Martin and Lindauer 1973).

Details of the Dance

Foragers do not signal the absolute distance to a source. For example, when there is a headwind, or the source is uphill, the dance indicates a greater distance (von Frisch and Lindauer 1955; Heran 1956). Adding small weights or drag-producing flaps to the forager produce the same effects as a greater distance (Schifferer 1952). When foragers are forced to walk rather than fly to a food source, a far greater distance is indicated (Bisetzky 1957). Distance, then, seems to be partially a measure of effort. On the other hand, when foragers from an Italian colony

were trained to fly up a 50 m radio tower or a 76 m bridge, only round dances were performed even though waggle runs normally begin at much shorter (horizontal) distances (von Frisch 1967a, pp. 167-168).

The distance correlation of the dance varies between races of honey bees (Lindauer 1961). The Egyptian honey bee, A. m. fasciata, begins signaling direction at only 10 m, whereas the Italian honey bee, A. m. ligustica, changes from round dance to waggle dance at about 35 m. Von Frisch's Carniolan bees, A. m. carnica, make this transition at 85 m. In an interesting experiment, one of von Frisch's students mixed two races in a hive to see whether recruits of one race would misinterpret the distance indicated by foragers of the other race. The results, regrettably, are inconclusive (Steche 1954; Boch 1957; in Boch's more extensive studies, recruits were given a choice between stations nearer and farther than the forager station. In all, 644 recruits arrived at the stations predicted on the basis of differences in racial dialects, but 667 arrived at the alternative station.)

Although von Frisch found dance tempo to be the most convenient measure of distance, several other components are also correlated (von Frisch 1967a, pp. 97-104). The least accurate measures include dance location in the hive -- the distance from the entrance to the dance correlates with the distance from the hive to the source -- and simply the physical size of the dance. The most accurate measure could be the duration of sound production during the waggle runs (Esch 1961; but see Wenner, et al. 1967). These bursts, which will be dealt with later in more detail, occur at about 30 Hz. Although the exact burst rate is correlated with the sweetness of the food (Esch 1963) and/or temperature (Wenner, et al. 1967), the number of bursts per run is also a reasonably good measure of distance. Both the number of waggles per cycle (the waggle rate is 13 Hz) and the duration of wagging are fair measures of distance, even though waggle runs often do not have a clear beginning and ending. The duration of an entire dance cycle, which includes both the waggle run and the semicircular return, is a somewhat less accurate indication.

The "vivacity" of the dance -- the sharpness and lateral extent of the wagging, the total number of cycles performed, and, basically, just how "excited" the dancer seems to be -- correlates with the relative quality

of the food (von Frisch 1967a, pp. 236-246). The dancer judges the quality of a source from the "reception" it receives in the hive -- that is, the amount of time required to "unload" the food to other bees. When more than about a minute is required to distribute a load brought back to the hive, the forager will usually not dance (Lindauer 1954). For example, water -- which is used to air condition the hive -- is normally not well received by the colony. If the day gets hot, however, foragers returning with very sweet nectar will no longer be able to distribute their loads quickly. Bees gathering dilute nectar or water, on the other hand, will be relieved of their loads very rapidly. The nectar foragers will stop dancing, while the water collectors will begin to dance vigorously. Bees in a colony regularly exchange food -- a process known as "trophollaxis." As a result, the hive may be thought of as possessing a "communal stomach," so that each bee is "aware" of the colony's supply of nectar and water. When, for example, Nixon and Ribbands (1952) fed radioactive nectar to a forager, most of the bees in its hive were radioactive in only a few hours. (The implications for colony susceptibility to pesticide-contaminated food brought back by only a few workers are clear.)

Dancing is performed under other circumstances as well. When the hive divides, about half of the bees fly out with the old queen and cluster in a swarm under a tree branch. Foragers fly out and search for suitable cavities to establish a new colony. When they return to the swarm, they perform dances on the cluster which correlate with locations of cavities in which to establish a new colony (Lindauer 1961).

Recruitment without Dancing

Many flowers produce nectar only at particular times of day or at certain temperatures. When a source stops producing food, the bees which have been foraging it may either switch to other flowers, or simply "rest" in the hive. These foragers may be re-recruited to the original source without having to attend dances. When the odor of the food which they had been foraging is put into the hive, some foragers will fly out to the original source. Experienced foragers can recognize the odors of a familiar source either in the air or on the bodies of other bees, and be recruited (Ribbands 1954; von Frisch 1967a, pp. 23, 30-35, 152-153).

Locale odor may be an important aspect of this recognition. In a typical experiment, von Frisch (1967a, pp. 152-153) trained two groups of foragers, one to a station in a field, and another to a station on the shore of a lake. The odor which was added to the food was identical at both stations. When the food was removed, many of the foragers "retired" to the hive. Foragers would occasionally appear at the stations, find no food, and return to the hive. When the food was replaced at one station, the first bee to "monitor" the site found the food, fed, and returned to the hive. Once back, the bee began to dance, but attracted only the most cursory notice from many members of the two groups of experienced foragers. Despite their inattention to the dance, most of the foragers from the dancer's station flew out to the food, while most of the foragers from the other station did not leave. Since most of the experienced bees did not follow the dance, those which flew out to the food must have been recruited by the odors on the dancer. Since the food odor was the same at the two sites and yet the dancer was unable to recruit most of the other station's foragers, at least one odor must have been wrong or missing. This difference probably involved the locale odors (see von Frisch 1967a, pp. 95-96, for another example).

Accuracy of the Dance

The many waggle runs in a dance are not identical. As Figure 3 indicates, when the source is relatively close, the direction of waggle runs alternates to the right and left of the "proper" orientation. Even when the source is very far away, the directions of various waggle runs are "scattered." Although the average of many individual runs gives the direction of the source, some runs are wrong by as much as 30°. Similar scatter is found in the indication of distance (von Frisch and Jander 1957).

The "noise" in the dance correlations led von Frisch to wonder how accurately recruits search for the food source being indicated by the dancing forager. He tested the direction accuracy by training foragers to one station, and then setting out a fan-shaped array of stations, each with the odor of the forager food (Fig. 6). Recruits were counted as they approached the stations, but were only captured at the forager station.

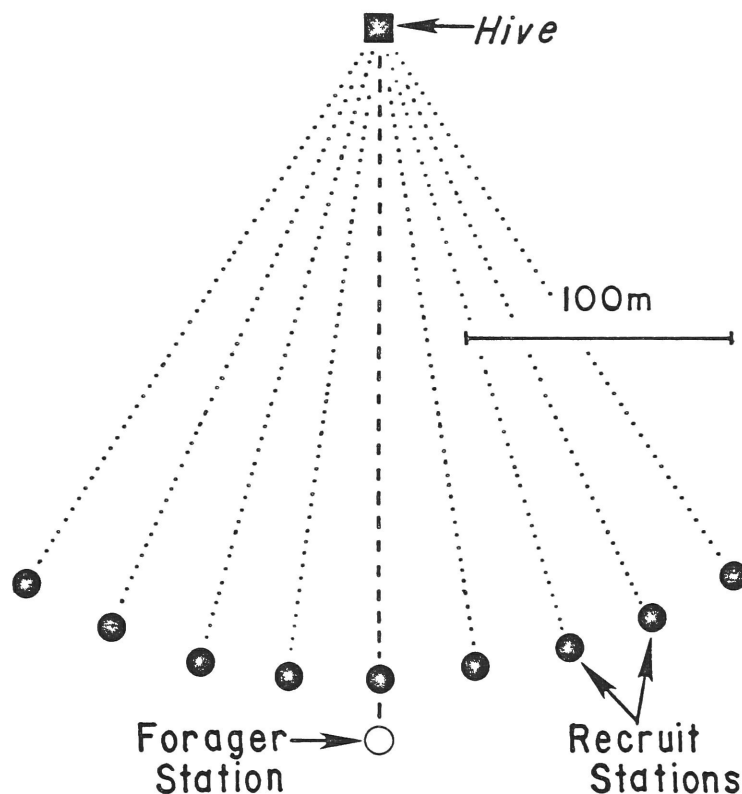


Fig. 6. A von Frisch "Fan" Experiment. Foragers were trained on a dilute, unscented sucrose solution to the location shown ("Forager Station"). During the experiment they were fed a concentrated, scented solution to elicit dancing and recruitment. Pieces of filter paper saturated with the scent were set out in an arc-like array of Recruit Stations. Recruits approaching these stations were counted but were not captured. Recruits arriving at the Forager Stations, on the other hand, were killed. Recruits favored the direction of the forager station (see data in Fig. 7). The wind was from a variety of directions. Redrawn from von Frisch 1967a, p. 161.

Hence, a recruit could be counted more than once. (Von Frisch feels that this procedure allows the "certainty" and "determination" of recruits to be taken into account. That recruits were counted more than once seems clear from von Frisch's [1947] observation that many more recruits were counted at some recruit stations than were captured at the nearby and more attractive Forager Station.) The results of 12 such experiments are combined in Figure 7 (von Frisch 1967a, pp. 156-161). Half of the recruits arrived within $\pm 7^\circ$ of the forager station. The number of bees arriving at the forager station was not reported. Since these recruits must be counted in order to estimate the accuracy, the 7° figure is an underestimate.

Von Frisch also performed a number of "step" experiments to see how accurately recruits arrived in a distance array (Fig. 8). As Figure 9 indicates, half of the recruits were observed within $\pm 2\%$ of the distance of the forager station (von Frisch 1967a, pp. 84-96). If only the recruits arriving at recruit stations are considered, the median accuracy is reduced to $\pm 10\%$.

How Unique are Honey Bees?

Although the existence of distance and direction information in the honey bee dance still seems remarkable nearly thirty years after von Frisch's original discovery, many of the phenomena involved are now known not to be unique to this single genus. Von Frisch's discoveries provided the "paradigms" which are said (Kuhn 1962) to facilitate further work along the same lines. Although none have been studied as thoroughly, many insects have behaviors which seem very similar to those involved in the honey bee dance.

The ability to use the polarized light of the sky for orientation has been demonstrated for more than 40 insect species, including a variety of bees, wasps, ants, flies, butterflies, and moths (Reviewed by Waterman 1973). The ability to transpose a direction taken with regard to the sun to a direction with regard to gravity has been noted for caddis flies (Jander 1960), the poplar-leaf beetle and Tenebrio (Tenckhoff-Eikmanns 1959), water striders (Birukow 1956), ladybirds (Tenckhoff-Eikmanns 1959),

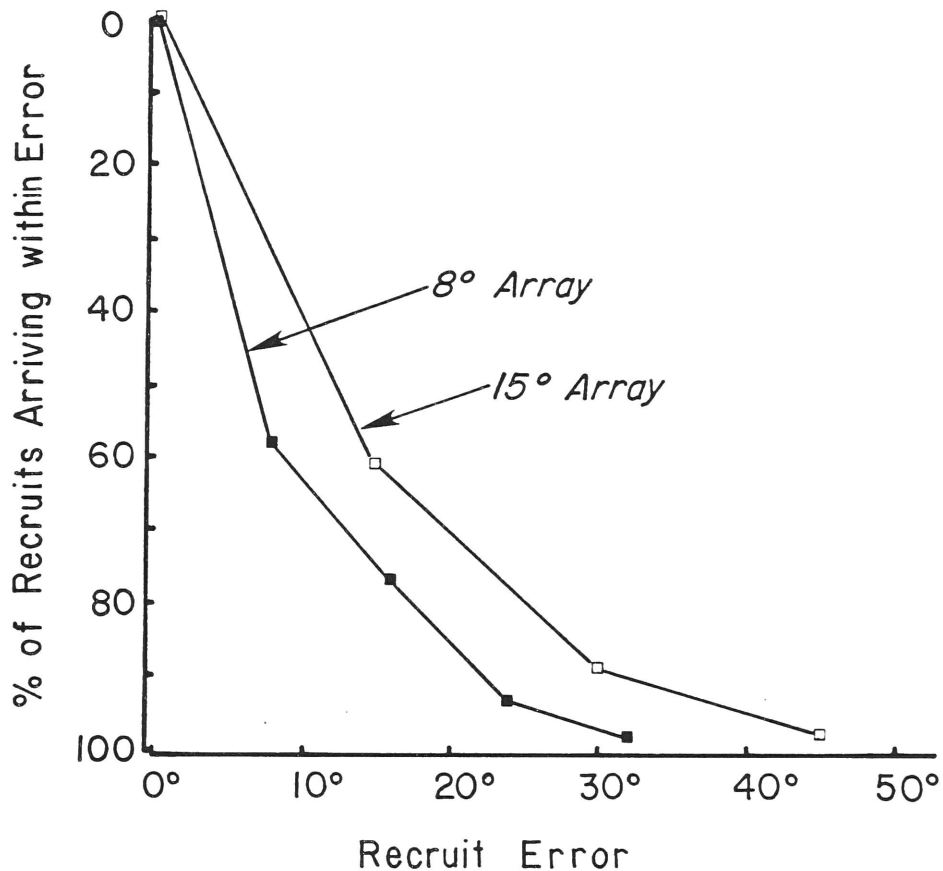


Fig. 7. Results of the Fan Experiments. The results of 12 fan experiments (based on data in von Frisch 1967a, pp. 156-161) are combined to examine recruit accuracy. Since the distribution of recruits seems to be partially a function of the angular intervals in the array, or its distance from the hive, data from experiments with 15° and 8° arrays are plotted separately. Since the number of recruits arriving at the Forager Station is not reported, the curve must be considered to be abnormally flat. In the 8° arrays, half of the recruits arrived within $\pm 7^\circ$ of the Forager Station.

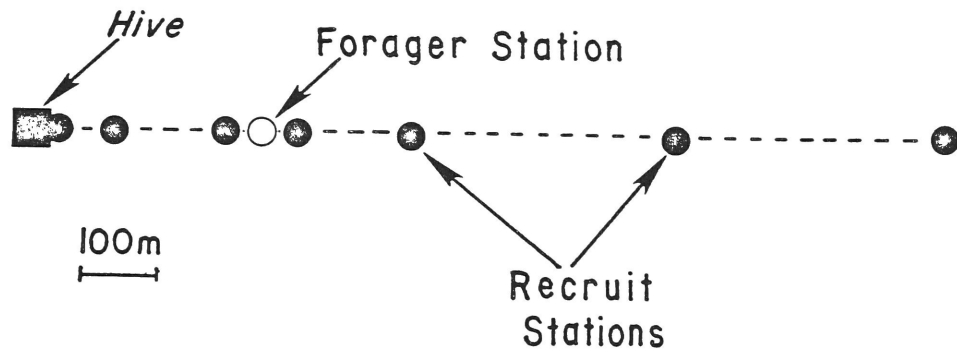


Fig. 8. A von Frisch "Step" Array. Foragers were trained on an unscented, dilute sucrose solution to the Forager Station. During the experiment they were fed a scented, concentrated solution to elicit dancing and recruitment. Pieces of filter paper saturated with the scent were set out as Recruit Stations at various distances. Recruits arriving at the Forager Station were killed, while those visiting the Recruit Stations were merely counted. Recruits favored stations near the Forager Station (see data in Fig. 9). The wind was from a variety of directions. Redrawn from von Frisch 1967a, p. 88.

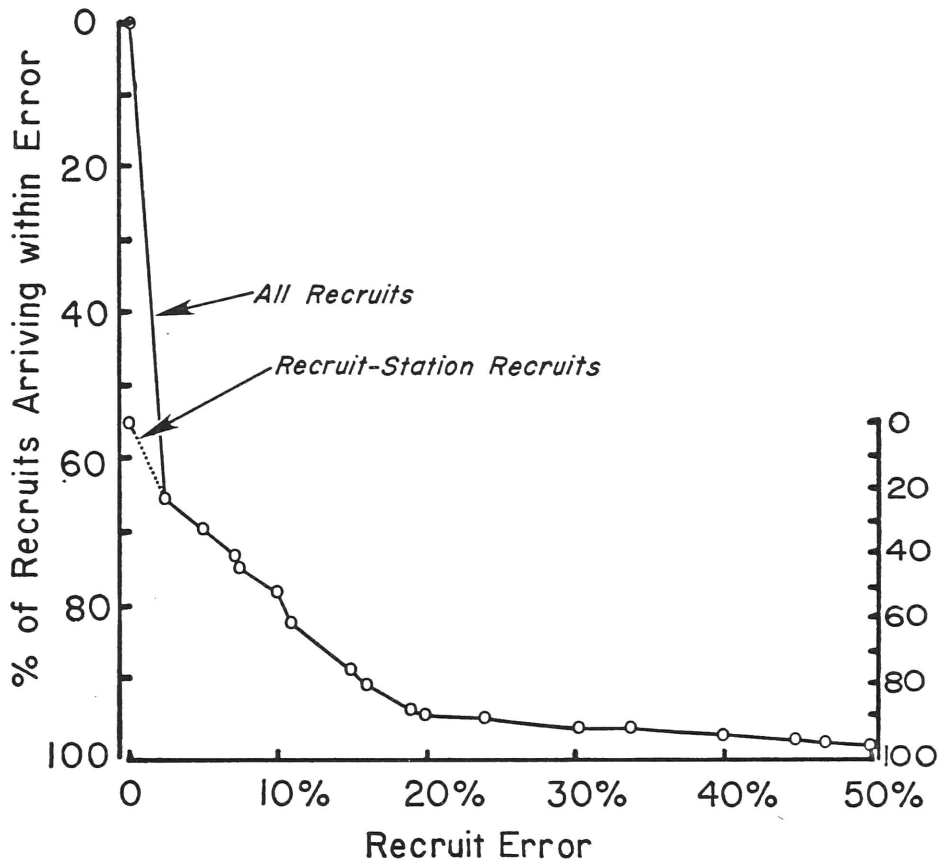


Fig. 9. Results of Step Experiments. The results of 7 step experiments (based on data in von Frisch 1967a, pp. 84-96) were combined to judge recruit accuracy. The left axis is for the solid line, the data for which includes the recruits arriving at the Forager Station. The right axis is for the dashed line, the data for which excludes the Forager Station. Since the size of the distance array was varied widely, accuracy is represented in % of the Forager Station distance. When the Forager Station data is included, half of the recruits arrive within $\pm 2\%$ of the goal, while an accuracy of $\pm 10\%$ may be inferred when the Forager Station data is excluded. Results from two experiments considered by von Frisch to have been unsuccessful are omitted.

ants (Markl 1964), and dung beetles (Birukow 1954). (Some of these insects, however, confuse left and right.) The functional significance of this behavior, if any, is unknown.

The ability to integrate an indirect path into a "bee line" has been found in ants (Jander 1957; R. Wehner, per. comm.), and spiders (Görner 1958). The ability to compensate for the sun's motion has been found in ants (Jander 1957; R. Wehner, per. comm.), sand fleas (Pardi and Papi 1952), and a long list of other arthropods summarized by von Frisch (1967a, pp. 444-451).

The capacity to transform distance travelled into duration of wagging or sound production has been observed until now only in moths (Blest 1960) and stingless bees (Esch, et al. 1965; they found that returning foragers moved through the hive performing "buzzing runs" similar to the acoustic position of the waggle run of honey bees. The duration of sound production was correlated with the distance to the food). The use of a dance and food regurgitation has been seen in ants (summarized in Wilson 1971), stingless bees (Esch 1967), termites (Lüscher and Müller 1960), and even flies (Dethier 1957).

Are von Frisch's Experiments Conclusive?

Many social and non-social animals "dance" excitedly after finding food, transform orientation angles from light to gravity, and convert distances travelled into durations of vibrations or sound production, and yet are not thought to communicate anything by these manoeuvres. Unsurprisingly, the question finally arose whether the evidence is really convincing that honey bees are uniquely endowed with a language. Wenner (1971) argues that although cricket songs correlate rather well with temperature, they are not thought to communicate that information to other crickets. (The apparently functionless "buzzing runs" of stingless bees is a more powerful example.) Indeed, wind speed and direction, temperature, and even humidity can be deduced from the honey bee dance (Wenner, et al. 1967), but no one has suggested that recruits use this information. The critical question, then, is not whether distance and direction correlations exist in the honey bee dance, but whether this abstract information is communicated to recruits.

Our failure to imagine any other function for the dance behavior (Lindauer 1971) should not be considered as conclusive evidence for communication. Of course, the dance language is wholly unnecessary for other bees, which are nevertheless able to exploit their environment quite efficiently. For example, when Lindauer and Kerr (1968) compared recruitment efficiencies of the honey bee and 10 species of meliponines (stingless bees), the honey bee only came in fourth. (On the other hand, had the experiments been done at greater distances, the communication system of stingless bees might have failed completely [Michener 1974, p. 153].)

Since honey bee recruits seem to know the general location of the food source being visited by a forager, the original olfaction theory is not a complete explanation. As mentioned previously, recruits have at least three other sources of information available to them: odor and visual cues left near the source by foragers; locale odors brought back to the hive on the body of the forager; and the symbolic distance and direction information in the dance.

THE DANCE-LANGUAGE CONTROVERSY

Wenner's Attack

Wenner (1967) and Johnson (1967a) designed experiments similar to von Frisch's step and fan experiments, but added controls for odor and visual cues left in the field by the foragers. Their results suggest that these clues alone account for the apparent accuracy of recruits.

Johnson (1967a) trained a group of foragers from his experimental hive to the forager station (Fig. 10) and set out three recruit stations with the same food. In contrast to von Frisch's technique, recruits were captured and counted as they arrived at the stations. The recruits were found primarily in the direction of the forager station (Table I, line A). Although this agrees with von Frisch's data, recruits might have used cues created by the foragers in the area of the forager station. To equalize odor and visual cues at the various stations, Johnson repeated the experiment with foragers from a second ("control") hive visiting the recruit stations. The bees from the control colony had a much lighter body color.

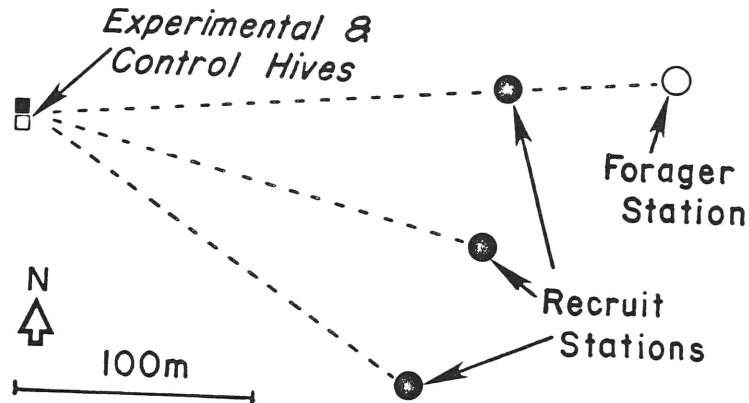


Fig. 10. Johnson's Fan Array. Foragers from the Experimental Hive (a colony of dark-colored bees) were trained on a concentrated and heavily-scented sucrose solution to the Forager Station. Foragers from the Control Hive (a colony of light-colored bees) were trained in the same manner to the Recruit Stations. No change in the feeding solutions was made for the experiments. Recruits arriving at all stations were killed. During the first experiment the Control Hive was closed so that only the experimental foragers were active. As expected, recruits favored the direction of the Forager Station (Table 1, line A). When the control foragers were allowed to frequent the Control Stations, however, thereby providing the sight of bees as well as bee, hive, and scent gland odor at all stations, this preference disappeared (Table 1, line B). In fact, the distribution of Experimental Hive recruits was very nearly the same as that of the Control Hive recruits (Table 1, line C). The wind was from 140° at 8 knots. Redrawn from Johnson (1967a).

Table I

	Forager Station	Recruit Stations (angle from Forager Station)			Total Recruits
		0°	20°	40°	
A	56%	22%	14%	8%	36
B	19%	21%	52%	8%	125
C	10%	18%	57%	16%	351

Table I. Results of Johnson's Direction Experiment. Line A: Recruits when only the Experimental Hive was open. Line B: Recruits from the Experimental Hive when both hives were open. Line C: Recruits from Control Hive when both hives were open. When foragers were only allowed at the Forager Station, the recruits favored the direction of the Forager Station -- presumably the direction of the dancing. When foragers were present at all stations, however, the distribution of recruits did not reflect the direction of dances in the hives (see text). Data from Johnson 1967a.

Hence, the colony to which recruits belonged could be determined as they arrived in the field.

Since the same number of foragers visited each station, the visual and odor cues were nearly identical at each station. Foragers from the control hive collected food in three directions, and stimulated bees from their hive to search in all three directions (Table I, line C). Foragers from the experimental hive, on the other hand, collected food in only one direction. If direction information is communicated by the dance, the recruits from the experimental hive should have been found mostly in the direction of the forager station. If, instead, they depend on cues left by foragers, they should not have been able to distinguish between the four stations. As the results indicate (Table I, line B), the experimental bees showed no preference for the direction of the forager station. Apparently, the information in the dance was not used.

Wenner (1967) used the same techniques to repeat von Frisch's step experiments. Foragers from the experimental hive visited a single station, while food with the same odor was offered at several stations at other distances (Fig. 11). Again, under these conditions, recruits favored stations near the forager station (Table II, line A).

Wenner then attempted to control for the forager-generated visual and odor cues which might be biasing the results. Once again, foragers from a control hive of light-colored bees were trained to the recruit stations. Recruits from the control hive arrived at all stations, as expected (Table II, line C). If recruits from the experimental hive used the distance information in the dance, they would be expected to arrive primarily at or near the forager station. If, on the other hand, they used only the cues left in the field by forager bees, recruits should be unable to distinguish between the stations. In fact, the experimental hive recruits showed no preference for the forager station (Table II, line B). Again, the dance information was apparently not being used.

In many ways, the experiments of Wenner and Johnson are not strictly comparable to those of von Frisch. The step and fan experiments were not designed to test so much whether honey bees have a dance language, but rather the emphasis was on how accurately it was used. The existence of a language was at least tentatively presupposed.

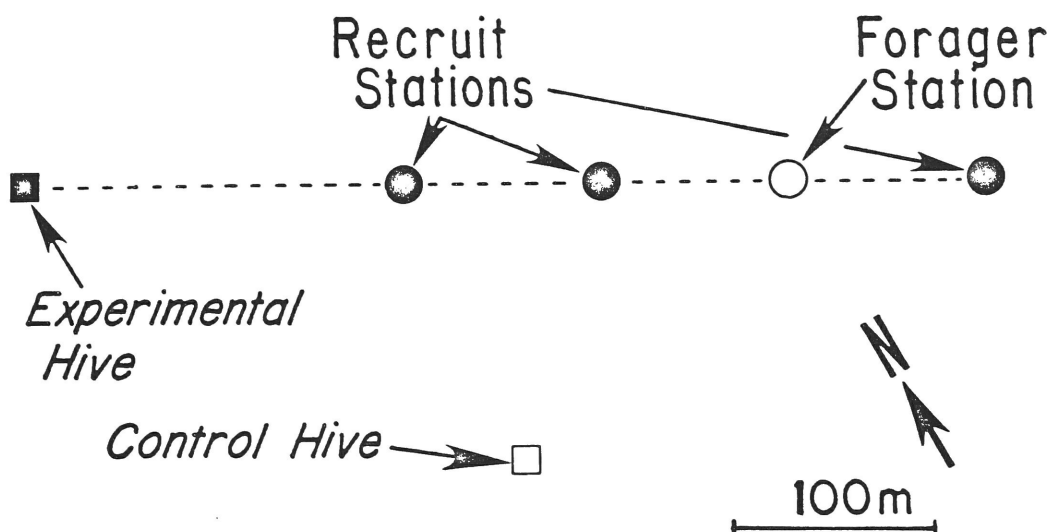


Fig. 11. Wenner's Step Experiment. Foragers from the Experimental Hive (a colony of dark-colored bees) were trained to the Forager Station on a heavily-scented concentrated sucrose solution. Foragers from the Control Hive (a colony of light-colored bees) were trained in the same way to the Recruit Stations. No change in the solutions was made for the experiments. Recruits arriving at all stations were captured and killed. When only the Experimental Hive was open, recruits arrived at or near the Forager Station, as expected (Table 2, line A). When the Control Hive foragers were allowed to frequent the Recruit Stations, however, thereby providing bee, hive, and scent gland odors as well as the sight of bees at all stations, this preference disappeared (Table 2, line B). The Experimental Hive recruits, in fact, showed the same distribution as the Control Hive recruits (Table 2, line C). The wind was from 220° at 9-10 knots. Redrawn from Wenner 1967.

Table II

	Recruit Station (200 m)	Recruit Station (300 m)	Forager Station (400 m)	Recruit Station (500 m)	Total Recruits
A	10%	14%	74%	2%	123
B	18%	48%	33%	1%	146
C	12%	62%	26%	0%	448

Table II. Results of Wenner's Distance Experiment. Line A: Recruits when only the Experimental Hive was open. Line B: Recruits from the Experimental Hive when both hives were open. Line C: Recruits from the Control Hive when both hives were open. When foragers were only allowed at the Forager Station, the recruits favored the Forager Station -- presumably the distance indicated by the dancing. When foragers were present at all stations, however, the distribution of recruits did not reflect the distance being signalled by dances in the hives (see text). Data from Wenner 1967.

Von Frisch Replies

Von Frisch (1967b) began his answer to the attacks of Wenner and Johnson by discounting the notion that recruits can use cues left in the area by foragers, at least at the distances that would have to be involved (see also von Frisch 1967a, p. 224). This argument depends on several untested but intuitively plausible assumptions. One assertion is that recruited bees fly to the food source with "surprising speed." The references cited, however, provide no way to judge how quickly recruits find a source. Three subsequent studies discussed later (Esch and Bastian 1970; Gould, et al. 1970; Mautz 1971) have dealt with this question directly. Although bees fly 100 m in about 13 sec. (Park 1923; Schifferer 1952; von Frisch and Lindauer 1955; Boch 1956; Heran 1956; Wenner 1963), newly stimulated recruits, if they find the food source at all, usually take 10 minutes or more to travel the same distance.

A second assertion is that the scent gland is not very important, since recruits do nearly as well when the foragers' glands are sealed shut with shellac. Unfortunately, shellac is also a potent odor cue for recruits. Elsewhere, von Frisch (1967a, pp. 22-23) reports that bees recruited by foragers with shellac-sealed glands arrive at and land on the bottles of shellac, rather than the heavily-scented food. Since shellac odor was present only in the vicinity of the forager station, these experiments do not rule out olfactory recruitment.

Finally, von Frisch states that other odor cues are "local," and hence of no importance in recruitment. Unfortunately, there is no data on the distance at which honey bees can detect pheromones or other odors. The ability of moths to orient to pheromones from thousands of meters away demonstrates that some insects are very sensitive to odors (Schneider 1974). (Von Frisch [1967a, pp. 95-96] relates one suggestive anecdotal incident. A "step" experiment was ruined because the odor from a spilled vial of lavender scent "flowed" out of a car as it moved along a road on which the experiment was later performed. Bees in this case were distracted by an odor hours after it had escaped from the automobile. The concentration of the odor must have been very low indeed.)

Von Frisch continued his reply to Wenner and Johnson by citing some of his other experiments as proof of a dance language. Unfortunately, none of these are particularly conclusive. In his "detour" experiments, von Frisch (1967a, pp. 173-186) trained his foragers along an indirect route to the forager station. Although they apparently remained faithful to the indirect path, the foragers signalled the actual straight-line direction in their dances. A few bees, presumed to be recruits, approached a scent plate set out along the "bee line" to the food source.

In the most elaborate of these experiments, the food source was on the opposite side from the hive of an 11-story building (von Frisch 1967a, pp. 179-180). Foragers were trained to fly around the building, but their dance directions pointed directly toward the structure. Three scent plates were set out on the building's roof -- one directly between the hive and food, and one at each end. Bees approaching the scent plates were not captured, and therefore could have been counted several times. Recruits arriving at the food, however, were killed. Of the 26 "approaches" recorded on the roof, 20 were at the station in line with the hive and food. Ninety bees were killed at the food station. Although von Frisch interprets the results as favoring the dance-language theory, the same distribution might have been observed if recruits had been flying out in random directions. Bees flying toward the ends of the building would be faced with the choice of flying slightly to the side and around the building -- a detour of 5 m -- or of flying up and over the 35 meter-high building. The small number of bees at the top of the end of the building does not really constitute proof of a dance language.

In another experiment, von Frisch (1967a, pp. 153-155) trained a group of foragers to a station 250 m to the south. The hive was laid on its side so that the comb would be horizontal, removing the gravity cue which normally orients dances in the dark. The dances became disoriented. Thirteen scent plates were set out, 4 to the south, and 3 each to the north, east, and west (Fig. 12). For the 90 minutes that the dances were disoriented, recruits arrived at all stations, but favored the stations to the north. Although the dances contained no information about direction, the distance correlation was essentially unaffected. Nevertheless, recruits

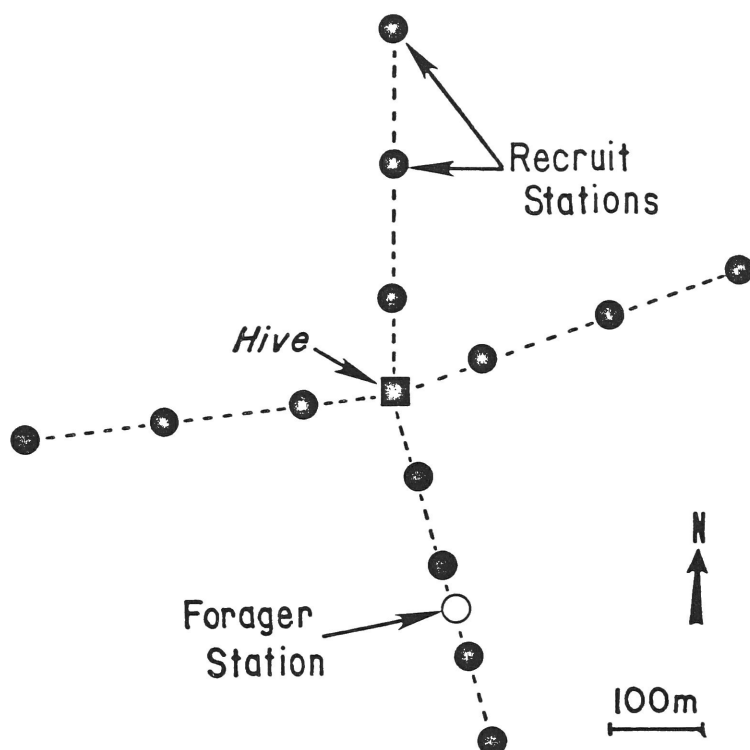


Fig. 12. Von Frisch's Horizontal/Vertical Hive Experiment. Foragers were trained on an unscented, dilute sucrose solution to the Forager Station. During the experiment a concentrated, anise-scented solution was used. For the first half of the experiment the hive was placed on its side, thereby removing the gravity cue to which foragers normally orient their dances. Although disoriented, the dances nevertheless contained consistent distance information. No preference for the correct distance was observed at the Recruit Stations. (What was done with these recruits, if anything, is not stated.) Later, after the hive was returned to the normal, upright position, recruits favored the stations near the Forager Station (see text). In a repetition of this experiment (Wells and Wenner 1973), recruits favored the area of the Forager Station regardless of the position of the hive. Redrawn from von Frisch 1967a, p. 154.

showed no preference for the correct distance. For the north, east, and west stations, 87 recruits arrived at 100 m, 69 at 250 m, and only 6 at 400 m. Von Frisch does not mention whether the recruits were captured, so that it is possible -- even likely in view of his normal protocol -- that bees could have been counted more than once.

Later in the day, the hive was set upright, restoring the direction orientation to the dances. After allowing 30 minutes for "transition," recruits were found almost exclusively to the south: 35 at 100 m, 40 at 200 m, 68 at 300 m, and 31 at 400 m. This experiment seems to suggest the use of a dance language. As so often happens, however, the footnotes contain disturbing details. The station directions were not exactly north, east, south, and west. The "conditions of the field" required that they be displaced up to 20°. Although the various "conditions" are not revealed, another footnote mentions an apple orchard between the hive and the station 100 m to the north. In order to explain a minor anomaly in the data, von Frisch mentions that the wind was from the north. The velocity, and how it varied as the experiment progressed, were not stated. Von Frisch also fails to report whether the scent glands of the foragers were sealed, whether the dancing and gland exposure varied during the experiment, whether recruits were captured, and how many bees were killed at the Forager Station.

From the details of this single experiment, it is impossible to exclude the possibility that odor cues alone could account for the results. (Von Frisch alludes to less elaborate versions of this experiment. It would be valuable if their details would also be published.) Alternative explanations abound. For example, since natural nectar sources are more attractive to bees than the artificial ones set out by experimenters (von Frisch 1967a, p. 18), when natural sources are available, foragers trained to artificial sources are less likely to dance (von Frisch 1967a, pp. 236-256) or evert their scent organs. Since many plants produce nectar only at particular times of the day (Parker 1925; Beutler 1930; Kleber 1935; Beutler and Wahl 1936; Butler 1945; Hammer 1949; Maurizio 1953; Huber 1956), this competition varies during the day. Since no controls were performed, it is entirely possible that the second part of the experiment might have had scent gland odor and more vigorous dancing (cf., Boch 1956). The

scent gland odor in the afternoon would account for the preference for the area of the Forager Station.

Similarly, the direction of the wind affects recruit distribution (von Frisch 1967a, pp. 96, 155, 156-161). The northerly wind would have blown hive odors along the array to the south -- the direction of the Forager Station. Since the direction and velocity of the wind can (and usually do) change during the course of a day, this factor must be taken into account when it is not otherwise controlled for by the design of the experiment. Indeed, the enhanced recruitment to the 300 m station is just what would be expected from a northerly wind blowing the odors from the Feeding Station to it. A plausible scenario might be that recruits searching for the food odor were first attracted upwind to the northerly line of scent plates. Since the recruits had failed to locate the food upwind in the morning, and since they had not been captured, they might be expected to search elsewhere -- downwind for example -- in the afternoon.

Or again, since locality odor is also likely to vary during the course of a day (as plants open and close, temperature and humidity rise and fall, and experimenters trample the vegetation), an increase in locale odor unique to the south array of stations would serve to explain von Frisch's results: when there was no locale odor (in the morning), recruits were disoriented; but when there was locale odor (in the afternoon), recruits were able to locate the stations near the Forager Station.

This single experiment is suggestive, but again is (regrettably) not conclusive evidence for a dance language. In fact, as described later, Wells and Wenner (1973) performed a similar experiment several times and obtained completely different results. Recruits arrived primarily near the Forager Station whether or not the dances were disoriented. Similarly, New (1961) found that recruits arrived at the Forager Station even when the dances were disoriented.

Von Frisch continued his rebuttal by criticizing the methods of Wenner and Johnson. Von Frisch (1923; 1967a, pp. 17-20) trains his foragers on a low concentration of sucrose so that they will not dance in the hive and thereby recruit new bees. In many cases, no odor is used

in the training solution. This method is slow and risks losing the forager bees. Wenner (1961) trains his foragers on a concentrated sucrose solution with a strong odor. Training under these circumstances is quick and sure. Von Frisch (1967b) hypothesized that bees recruited by the dances of the foragers during training might not have been able to locate the station since it was being moved rapidly away from the hive toward the experimental location. This failure of bees recruited during training to locate the Forager Station "with surprising speed and accuracy" might be a serious source of error, particularly since Wenner continued to use the training odor during the experiment. As this odor accumulated in the hive, the potential for recruitment to the odor alone increased (von Frisch 1967a, pp. 257-264; Free 1969). Under such circumstances, of course, the dance language would be irrelevant. These differences in training technique -- sucrose concentration and scent -- become crucial later, and so should be kept in mind.

Von Frisch also attempted to explain the results of Wenner and Johnson on the basis of wind direction. He suggested that the southeasterly winds might have distorted the results. Von Frisch (1967a, pp. 156-161) had found in his own experiments that recruits are often "displaced" slightly upwind.

Von Frisch concluded by pointing out that his experiments often involved much greater distances than those used by Johnson and Wenner. In this regard, it may be useful to note that the hybrid strain used by the latter workers makes its transition from round to waggle dance at about 25 m, whereas von Frisch's Carniolan bees make the same shift at about 85 m (a fact which may have delayed the discovery of the correlations). This difference in scale between the two races may make the distance physiologically similar.

Wenner and Johnson Reply

In their answer to von Frisch, Wenner and Johnson (1967) ignored his criticisms, and dealt instead with their own ideas of bee communication and science in general. According to them, bees learn the odors from the dancers and, by a sort of conditioned reflex, fly out, drop downwind, and

search for the food. They mention the possibility that recruits might use locale odors in addition to the food odor and odors left in the field by the foragers.

Unfortunately, the discussion by Wenner and Johnson is marred by several factual errors. Like von Frisch, they describe the flight paths of recruits even though no technique exists for following single bees. They refer to the "repellency" of hive-specific odors from foragers of other colonies, even though this factor, were it important (e.g., Wenner 1968), would make the analysis of their own two-colony experiments very difficult. They state that sealing the scent glands of foragers is a useless control since newly arriving bees expose the organ before they land. Not only is this not true (Free 1968; Gould, et al. 1970), but even if it were it would hardly serve to explain how the recruits got there in the first place.

In their reply to von Frisch, Wenner and Johnson also considered the "philosophical" implications of the exchange, citing, among others, Thomas Kuhn and his Structure of Scientific Revolutions (1962). What considerations of this sort may or may not add to the evaluation of research will be discussed later.

Another Exchange

Johnson (1967b) went on to replicate von Frisch's experiments in which experienced foragers were re-recruited to a familiar source. Although he obtained the same results as had von Frisch, Johnson interpreted them as casting doubt on the dance language. Of course, by their design experiments of this sort emphasize the importance of food and locale odors.

In his caustic reply to Johnson's work, von Frisch (1968) pointed out the previous work and reiterated the dance-language interpretations. Unfortunately, von Frisch fell into the trap which Johnson had set. Von Frisch made several plausible but unproven assertions -- claiming, like Wenner and Johnson, to know the flight paths of recruits (based on the "detour" experiments), and failing to point out that since recruitment of experienced foragers does not require dancing (von Frisch 1967a, pp. 23, 30-35, 152-153; Free 1969), experiments of this sort have nothing to say

about whether or not there is a dance language. When von Frisch commented that "it is a pity that Johnson tried to investigate the importance of dancing with bees that never or seldom danced at all," he was being misled by Johnson's inappropriate and largely irrelevant conclusions.

ATTEMPTS TO RESOLVE THE DANCE-LANGUAGE CONTROVERSY

As Gould, et al. (1970) pointed out, the experimental methods of the Wenner and von Frisch groups are not sufficiently similar to allow comparison of their results. Each group makes certain assumptions about what is or is not "important" to bees. Many variables may affect foraging behavior, dancing, and recruitment. Since complete knowledge of these factors is lacking, adequate controls should be used for all of them. The significance of an abstract dance-language system in bees, if it really exists, is very great indeed. It represents, according to von Frisch (1967a, p. 57) "an accomplishment on the part of bees that is without parallel elsewhere in the entire animal kingdom." It has often been cited as the classic example of animal communication, and has been a favorite subject for philosophers and linguists for many years. The possibility that no symbolic communication is actually involved in honey bee communication has attracted considerable attention. Many interested scientists have weighed the evidence (Dawkins 1969; Michener 1969, 1974; Tavalga 1970; Wilson 1971; Griffin 1971; Altmann 1972; Thorpe 1974; Davenport 1974), while several new attempts at fully-controlled and conclusive experiments have been undertaken (Gonçalves 1969; Gould, et al. 1970; Esch and Bastian 1970; Lindauer 1971; Mautz 1971; Gould 1974). Given the remarkable ability of honey bees to learn and respond to odors, the newer experiments have sought to follow von Frisch's (1967a, p. 22) wise advice: "These complications [faint odors] must be kept constantly in mind if one wishes to avoid being deceived in experiments with bees."

Attempts to Control for Cues Left in the Field

The most elaborate of the several attempts to resolve the dance-language controversy was made by Gould, Henerey, and MacLeod (1970). Although their analysis of previous attempts to control for possible

olfactory cues illustrates their unfamiliarity with bees, it is also free of the bias of personal experience. Every odor, no matter how unlikely, was assumed to be important. Whether their attempts to control for such cues were effective is another question.

The experiments were performed in the high desert of eastern Oregon in order to eliminate natural sources of food, locale odors, landmarks, and the possibility of wild, indigenous colonies. The site was symmetrical and flat (Fig. 13). Foragers were trained by a variation of von Frisch's method (Gary and Witherell 1971) -- using a weak sugar solution without the experimental scent -- to each of two stations located 120 m from the hive in opposite directions. The foragers were individually marked, and their scent glands sealed with paint. Dancing in the hive was recorded. Recruits arriving at the stations were captured by a new method which precluded release of alarm pheromones.

Series I

In the first series of experiments, about half of the 8000 bees in the 1 1/2-frame observation hive were numbered. This time-consuming process was greatly expedited by taking bees at night from the upper frame of the hive, rather than by catching them at the entrance. The bees were chilled and tagged, then returned to the hive. Unfortunately, most of the bees tagged in this way were "housekeepers" -- bees in their first three weeks of life, and hence not yet foragers. Since the tags came off in time -- perhaps even before the bees began to fly -- the proportion of tagged foragers was far less than 50%.

In Series I, both groups of foragers were fed on a 2.5 M sugar solution. The dances in the hive were recorded, as well as the identification numbers of any bees which followed three or more waggle runs. The dances of the two groups of foragers differed only in direction. Recruit bees might observe either dance. If bees use the direction information in the dance, they should have been found predominantly in the direction indicated by the particular dance they happened to observe. If, on the other hand, only odors are important, the direction of the station at which any specific recruit arrives should show no correlation with the direction of the dance it had attended.

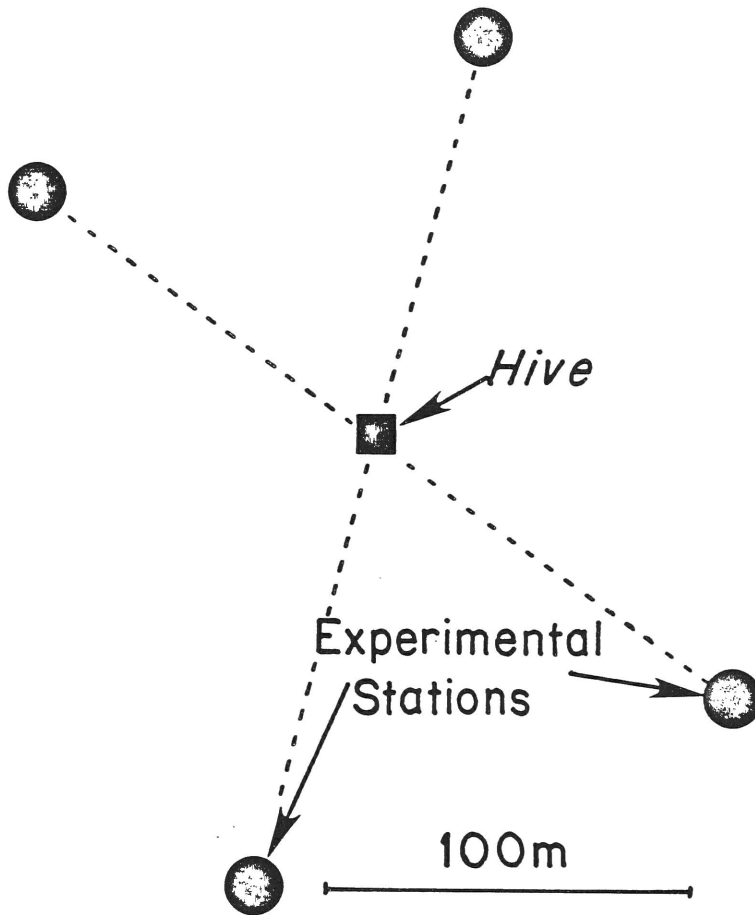


Fig. 13. Array of Gould, et al. Foragers were trained in opposite directions on a dilute, orange-scented sucrose solution. All recruits were captured. During Series I, both groups were fed a concentrated solution either without odor or containing peppermint scent. Recruits favored the station indicated by the particular forager whose dance they actually attended (Fig. 14). During Series II, only one group received the concentrated solution, although the food odor was the same at each station. Recruits favored the station indicated by the group of dancing foragers by about 20 to 1 (Table III). The wind was from a variety of directions. Redrawn from Gould, et al. 1970.

Since some of the captured recruits were uniquely numbered and had been observed following a dance in the hive, the possibility of a direction correlation could be tested. The results are presented in Figure 14. Recruits arriving at a station soon (< 4 min.) after observing a dance did very well -- 10 of 11 found the station whose direction had been indicated in the dance. Recruits which took a great deal of time (> 12 min) did no better than would be predicted by chance -- 6 of 12 in the dance direction. Recruits taking an intermediate amount of time had an intermediate amount of success -- 9 of 14 in the indicated direction.

Thirty-seven recruits in six hours of observation is certainly a slow way to gather data. Increasing the number of foragers would decrease the percentage of dances which could be recorded. In fact, the problem in interpreting the Series I data is that, as Esch and Bastian (1970) later showed, most recruits return time and time again from unsuccessful searches to attend additional dances. Since not all the dances could be recorded at once, recruits scored as taking longer times were probably just those whose most recent dance attendance had gone unnoticed. Of course, the probability is only 50% that the later dance had the same direction as the one which such bees had been recorded as attending.

An (unpublished) analysis of the Series I data indicates that most successful recruits had been recorded attending at least one earlier dance. As discussed below, this fits the pattern reported later by Mautz (1971) as well as Esch and Bastian (1970), but seems in sharp contrast to the statement that "recruits fly rapidly and with certainty to the food" (von Frisch 1967a, p. 57).

The problem with the Series I work was that two different sets of dances were going on simultaneously. Happily, the colony absconded, numbered tags and all, putting an end to this approach.

Series II

The second series of experiments, although giving no data on individual recruits, generated statistically significant numbers. The two groups of foragers were fed sugar solutions of different concentrations: the experimental group received a 1 M solution, while the control group was fed an 0.5 M solution. (When a greater concentration difference was employed,

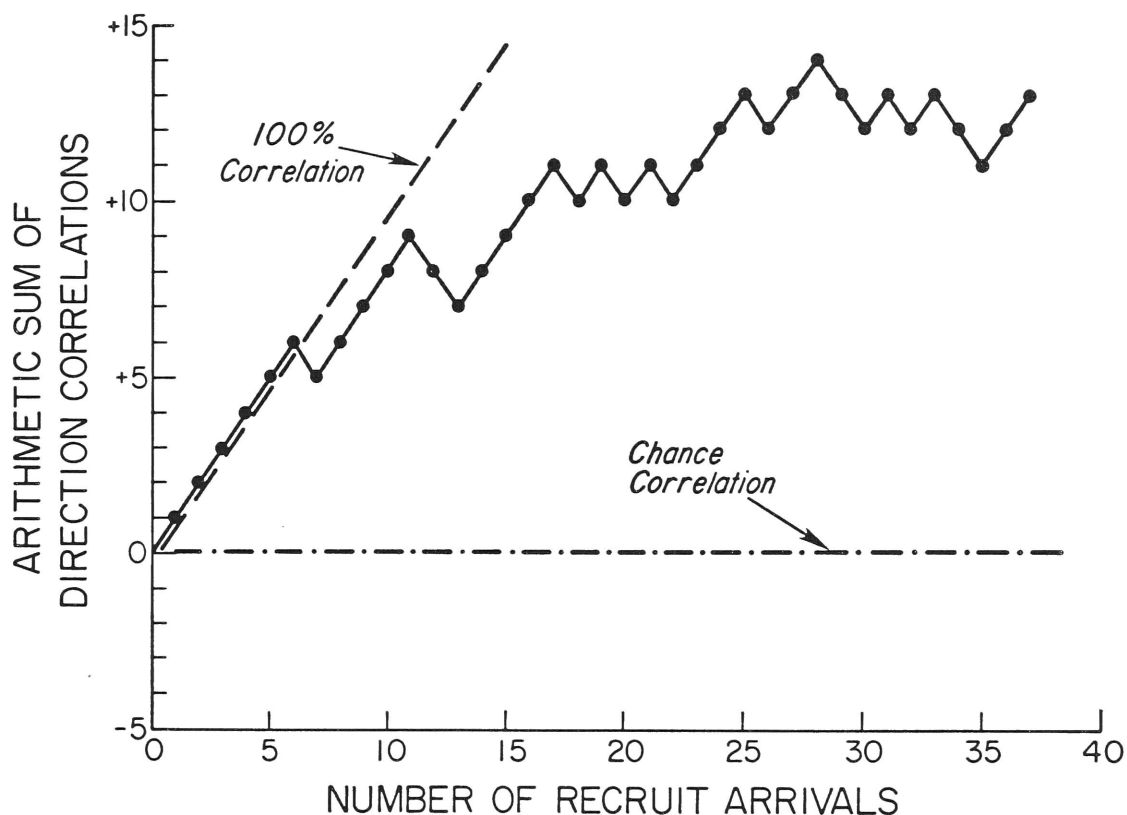


Fig. 14. Results of Series I. The direction of the station at which numbered recruits arrived is compared with the direction of the most recent dance they had been observed attending. A positive correlation is scored as 1, a negative correlation as -1. The curve represents the arithmetic sum of the correlations arranged in the order of increasing time interval between the dance and capture. Recruits arriving within 4 min. of a dance cause the curve to approximate the line of 100% correlation (dashed line [-----]), while those arriving 12 min. or more after being recorded at a dance cause the curve to parallel the line of random correlation (dot-and-dashed line [-.-.-.-.-]).

From Gould, et al. 1970.

the foragers from the second group were slowly recruited to the feeding station of the first.) Because dilute nectar does not release dancing, only the experimental foragers tended to dance. Of 562 dances observed, 526 -- 93% -- indicated the experimental station. Moreover, the 36 dances for the control station were noticeably less lively.

If recruits use the direction information in the dance, most of them should arrive at the experimental station. If, on the other hand, only odor cues are used and the stations had the same odor, the recruits should show no preference between the two stations. In fact, of 295 recruits, 282 -- 96% -- arrived at the experimental station (Table III).

The validity of these results depends on the success of the efforts to make the stations in every way equivalent. The similar rates of forager visitation (Table III) should have kept the amount of hive-specific odor and the degree of visual landing encouragement approximately equal. The apparent uniformity of the landscape should have limited or eliminated site- and path-specific odors. General site taxis -- any innate tendency to favor a particular direction -- was controlled internally in Series I, and through reversal of the experimental and control stations in Series II. By utilizing various orientations to the wind in each series, the effect of this parameter could be studied. Sealing of the scent gland precluded the release of that pheromone, while the odor of the paint used to seal the gland was the same at each station. The capture technique prevented the release of alarm odor. The disposal of experimental fluids and feeding containers every 10 minutes and the rotation of experimenters prevented the development of differences between the stations due to these factors as the experiment progressed.

In the presence of controls for each of these odors and biases, recruited bees were able to locate a food source indicated by the dances of returning foragers in preference to a food source located at an equal distance in the opposite direction. The results support von Frisch's dance-language interpretation.

However unlikely, one cannot rule out the possibility that recruits used some factor other than the dance-language information or the visual and olfactory cues for which Gould, et al. established adequate controls.

Table III

	<u>Foragers</u>		<u>Dances</u>		<u>Recruits</u>	
	Exp. Sta.	Con. Sta.	Exp. Sta.	Con. Sta.	Exp. Sta.	Con. Sta.
A	127	163	93	17	77	1
B	245	200	95	2	21	1
C	93	132	80	0	62	0
D	138	140	101	0	64	0
E	101	133	82	2	59	0
F	220	226	75	15	69	11
Total	924	994	526	36	352	13

Table III. Results of Gould, et al. Series II. Recruits visited the two stations with equal frequency, thereby offering an equal degree of olfactory and visual attraction to recruits. In the hive, however, dances predominantly indicated one station. 96% of the recruits arrived at the stations indicated by the dancing.

For example, there is no way to be sure that unique locale odors were not being used. As they pointed out, "a conclusive experiment might be one in which the information contained in the dance of the forager is altered in such a way that recruits using this directional information would proceed to a location to which the dancing forager had never been. To accomplish this, one would have to change the dancer's relationship to some pertinent environmental parameter without simultaneously altering the relationship for attenders."

Further Studies of the Behavior of Individual Recruits

Esch and Bastian's experiments

Even though Esch and Bastian (1970) never mention the controversy or cite Wenner's work, their experiments were clearly aimed at testing the existence of a dance-language system of communication. Their strategy was to follow the behavior of each individually marked recruit as it attended dances in the hive and subsequently arrived in the field. Their approach differs from that of the Series I of Gould, et al. in several important respects.

Esch and Bastian individually numbered 10 bees from a group foraging on scented sucrose near the hive. These 10 bees, already "pretrained" to the experimental odor, were kept in a cage while the rest of the group was trained to 200 m. All of the foragers but one were captured, and then the 10 marked bees were released. Esch and Bastian then observed the interactions of the marked bees with the single forager. The experiment was repeated seven times. Of the 70 marked bees, 34 attended a total of 89 dances -- 509 wagging runs by the foraging bees. Of these 34 bees, only 14 found the food source. Successful recruits attended an average of 6 cycles, flew out and presumably searched for 5 minutes, returned and followed 6 more cycles, and found the food after an additional 3 minutes of searching. Unsuccessful recruits typically followed 5 dance cycles before each of three fruitless searches; finally they gave up.

From their data, Esch and Bastian concluded that recruits had to follow at least three consecutive cycles of a dance to be able to locate the food. Observations of two arriving recruits suggested to them that

the location of the source was known "before leaving the hive." Only 4 of their 14 successful recruits located the food on a first flight.

Mautz's experiments

In another attempt to follow the behavior of individual recruits, Mautz (1971) gave unique numbers to 1000 bees in a colony of 4-5,000. He then trained single foragers to a food source, observing any interactions they had in the hive with numbered bees. In contrast to the experiments of Esch and Bastian, these numbered bees were not "pretrained" to the experimental food. Nevertheless, the results of the two experiments are similar.

Mautz found that only half of the bees which attended dances and flew out were successful in locating the food source. Just as in the experiments of Esch and Bastian, unsuccessful flights took about 7 minutes, while the subsequent successful flight required about half as much time. Again, successful recruits had observed at least 5 dance cycles.

Since bees fly at 7 m/sec (Park 1923; Schifferer 1952; von Frisch and Lindauer 1955; Boch 1956; Heran 1956; Wenner 1963), the time to reach a source whose location is known "before leaving the hive" should be about 30 seconds under the conditions of Esch and Bastian, 15 seconds for the Gould, et al. experiments, and 15, 30, and 60 seconds for Mautz's recruits. Since the average bee, if it found the source at all, typically took 18 times longer, the statement that recruits "fly rapidly and with certainty" (von Frisch 1967a) is subject to doubt. The recruits did not find the food rapidly, and since only one feeding station had been set out in both Mautz's and Esch and Bastian's experiments, the "certainty" of the recruits cannot be adequately judged.

Further Attempts to Control for Cues Left in the Field

Lindauer (1971) performed experiments virtually identical to the Series II of Gould, et al. (1970). He trained foragers to each of two stations located 200 m from the hive, but 90° apart (Fig. 15). When the experiment began, one group was fed a 1.5 M sugar solution, while the other was given a 0.125 or 0.063 M solution. Presumably only the foragers collecting the more concentrated food danced in the hive, but no

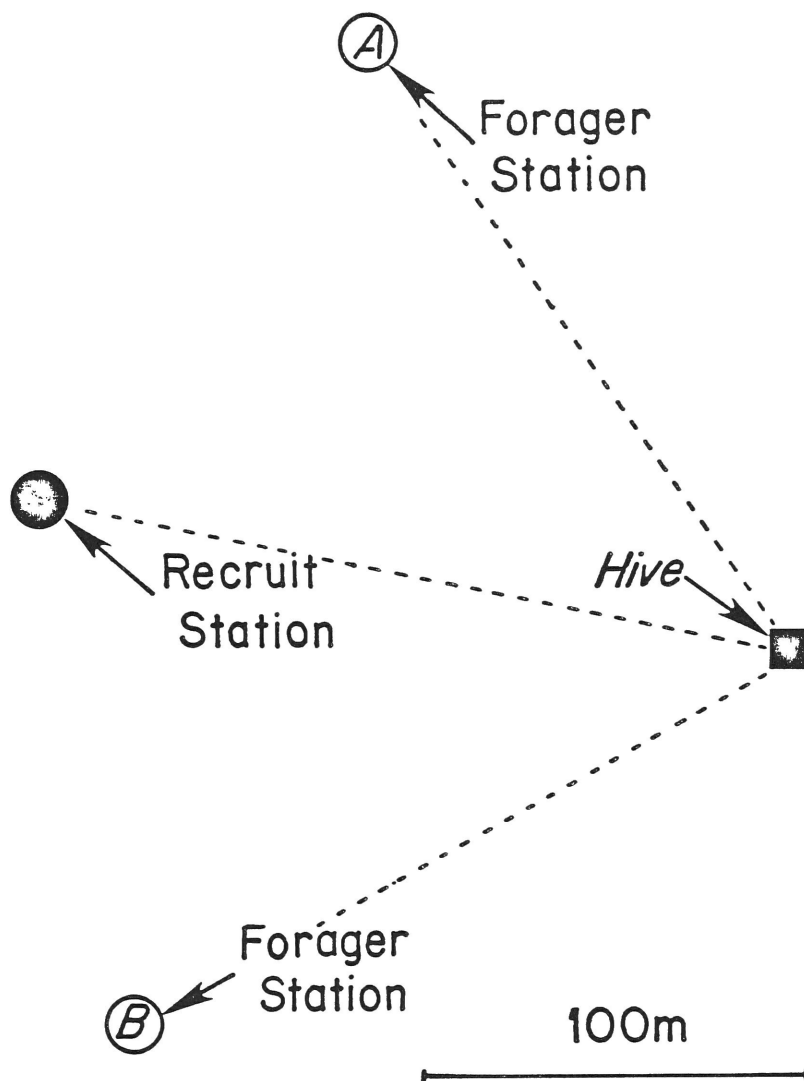


Fig. 15. Lindauer/Wenner, et al. Array. In Lindauer's first experiment, foragers were trained on an unscented, dilute sucrose solution to the two Forager Stations located 90° apart. Foragers at one station had their scent glands painted with shellac. During the experiment, the solution at the shellac station was more concentrated than that at the other station. Recruits favored the shellac station (see text). The same training procedure was used in Lindauer's second experiment. A third station was set out between the Forager Stations. A concentrated scented sucrose solution was offered at all three. Recruits favored the two Forager Stations (see text). In the Wenner, et al. experiment, foragers were trained to the Forager Stations on a concentrated scented sucrose solution. During the experiments, the scent was removed from the Forager Stations, but added at a third station located in between. Recruits favored this middle station (see text). Recruits were captured and killed in all three experiments. Wind in the Wenner, et al. experiment was generally from the bottom. The velocity was not stated. Wind in the Lindauer experiments was weak and generally from the right. Redrawn from Wenner, et al. 1969 and Lindauer 1971.

observations were made. Arriving recruits were captured and killed. Five experiments were performed. The station with the more concentrated food attracted 379 recruits versus 35 at the other station. (Although 379 is the figure cited in the text, the tables indicate that the actual number was 429.)

In order to control for the scent gland odor, Lindauer sealed the glands of the foragers visiting the 1.5 M station with shellac. Foragers collecting the more dilute solution did not expose their glands, and hence were not treated. Unfortunately, bees are very responsive to the odor of shellac, even to the point of ignoring the odor of the food (von Frisch 1967a, pp. 22-23). The bees which were supposed to have been dancing carried the odor of shellac. If recruits were relying on olfactory cues, they would find shellac odor only at the station with the more concentrated food. Hence, the results of Lindauer's experiments do not exclude the possibility that bees use odor cues alone.

THE DEVELOPMENT OF ALTERNATIVE THEORIES OF RECRUITMENT

The Wenner group remained active while the several efforts were being made by others to control for cues left in the field by foragers. Additional evidence was obtained implicating odor rather than language as the crucial cue. Later, two new theories of recruitment were developed, both virtually immune to testing.

The Olfaction Theory

Wenner (1968) summarized his view on recruitment in the context of a comprehensive review of honey bee communication. His olfaction theory, basically an extension of von Frisch's (1923), emphasized the role of "conditioned" responses to odors. Factors listed as important by Wenner include the food odor, the "characteristic odors of the location," the odor of the bees -- "the strongest single attractant" -- and scent gland odor. Wenner goes on to state that recruited bees "drop downwind from the hive and pick up the odors to which they have been recruited." Unfortunately, no evidence is cited. Once recruits have found a site with the correct odors, the sight of other bees encourages them to land.

Which Odor Cues are Important?

Wenner, et al. (1969) trained foragers to two feeding stations 200 m from the hive and 90° apart (Fig. 15). Although no direct observations were made, foragers were presumed to be dancing. Recruited bees were captured, counted, and killed. On some days, 1.5 M clove-scented sucrose was offered at the forager stations. On other days, the forager stations offered unscented 1.5 M solutions, while a third station located between the forager stations offered the clove-scented solution. Recruits were induced to land by placing small bee-sized pieces of sponge around the feeding dish.

On days when the forager solutions were unscented, the rate of scent gland exposure doubled. The center station, which alone offered the food scent from previous days, received 180 recruits, while the unscented forager stations attracted only 31 new bees. From these results, Wenner and his colleagues concluded that the sight and odor of foraging bees -- previously the "strongest single attractant" -- were only effective over very short distances. Further, they stated that scent gland odor does not "aid in recruitment of bees."

Wells and Wenner (1971) investigated the occurrence of scent gland exposure in more detail. There, they concluded that any forager which marked a source was aware through some unspecified sort of aerial encounter that "confused recruits" were searching for the forager's particular food source. Hence, the foragers mark a food source under these conditions just as they mark the hive entrance under other circumstances. Unfortunately, there is no direct evidence for this notion.

Wenner, et al. (1969) consider their experiments to be a conclusive test of the dance-language hypothesis. However, several aspects of the protocol and data are difficult to analyze. The food odor was 20 times more intense than the level typically used by von Frisch. Both hour by hour and day by day, the clove odor being brought back and stored in the hive grew stronger. Recruitment in the hive on the basis of odor alone is a distinct possibility. This is especially likely since on one day when the foragers were fed peppermint, 44 recruits nevertheless went to the clove station and only 2 to the forager stations. In addition, the rate of

recruit arrival increased dramatically over the three hours of the experiments in which foragers collected clove-scented sucrose, but remained constant on days when the unscented solution was being collected. Again, recruitment to odor alone is implicated: on the clove days, the odor level in the hive increased as foragers brought back additional scented solution, while on the unscented days, the odor in the hive from the clove-scented food stores must have remained relatively constant. Recruitment under these conditions was very low for a hive of 60,000 bees. Since the colony was not observed, the possibility that little or no dancing took place cannot be excluded. In an earlier experiment, Johnson (1967b) recorded only 30 dances by 60-100 foragers in 280 minutes of observation. The high concentration of odor in the food could have inhibited dancing (Kashev 1957), a phenomenon Wells and Wenner (1971) noted later.

Do Bees Integrate Dances?

Lindauer (1971) repeated the Wenner, et al. (1969) experiments with certain modifications. Although the physical arrangement of the stations was the same and no foragers were trained to the center station, the experimental scent was offered at all three sites (Fig. 15). No mention is made of whether the scent glands were sealed shut. The center station attracted 91 recruits, while the forager stations had a combined total of 349 recruits. Lindauer concluded that the bees which arrived at the center station had averaged the different directions of dances to the two forager stations. When the foragers fed on unscented sucrose while the earlier experimental scent was offered at the center station, Lindauer got entirely different results. In two experiments, only 6 recruits arrived at the center station while 223 found the forager station.

Lindauer's experiments are not strictly comparable with those of Wenner's group. Lindauer offered no visual landing encouragement at the foragerless center station. Lindauer does not state the size of his colony, but since he was able to observe some of the dancing it was probably an observation hive of no more than 10,000 bees -- much smaller than Wenner's. Lindauer's foragers recruited bees much more effectively than did Wenner's. The effect of this difference, however, cannot be predicted. In any case, Lindauer's results are explained equally well by either the olfaction or the dance-language theory.

The Importance of Locale Odor

By excluding several odors as unimportant, Wenner, et al. (1969) sharply reduced the previous list of potential cues (Wenner and Johnson 1967). Prominent survivors were food, hive, and locale odors. Later, Johnson and Wenner (1970) analyzed earlier data with this in mind. They attempted to demonstrate that recruitment is disproportionately enhanced by increasing the strength of the food odor. With 4 drops of scent per liter of food, 93 dances produced only 2 recruits. Food with 10 drops per liter elicited 145 recruits in response to 123 dances. Unfortunately, in the first case the scent was lavender two times out of three, while in the latter it was always clove. The comparative "strength" of odors may not be strictly a function of the quantity used.

It is also disturbing that the rate of dancing in the higher-scent series was nearly three times greater than with the lower scent. Dancing is inhibited by higher scent levels (Kashev 1957; Wells and Wenner 1971). If food stress or some other factor encouraged vastly more dancing despite the high odor levels, the higher rate of recruitment might not say as much about the effectiveness of scent as the effectiveness of hunger.

More significantly, Johnson and Wenner found that enhancing the site odor could have spectacular effects on recruitment. Foragers were trained to two stations in opposite directions, 150 m from the hive. 1.5 M peppermint-scented sucrose was offered at each site. 353 dances elicited 36 recruits -- divided evenly between the two stations. When the grass near one station was cut, thereby enhancing the locale odor, the rate of recruit arrival at that station increased eight-fold. On the next day the grass was cut at the other station with the same result. It must be added, however, that twice as many dances in the hive indicated the mowed site in one of the experiments.

Johnson and Wenner also determined that recruits follow approximately 7 dance cycles, then leave the hive within about a minute. Most dance followers, however, never located the food site. Recruits which did find the food took at least 10 minutes to do so. These data agree well with those of Gould, et al. (1970), Esch and Bastian (1970), and Mautz (1971) discussed earlier.

The Locale Odor Theory

Subsequent work generated additional anecdotal evidence for the importance of locale odor as a site-specific cue for recruits. In his book, Wenner (1971, pp. 65 ff) reported that nearby leaf litter, sun tan oil on a technician, trampled or cut grass, insecticide on a nearby hedge, and chicken manure between the hive and the feeding station all provided cues which greatly enhanced recruitment. He goes on to point out that locale odor could explain virtually every honey bee experiment without recourse to the dance-language theory.

Wenner also mentions that odors from a particular brand of paper towels had the same effect. This is consistent with the observation in my experiment 1, described later, that an unusually large number of recruits appeared at the forager station. Most of these bees ignored the feeding dish, investigating a newspaper lying 3 m away instead. The recruitment rate at the station fell when the newspaper was removed. Newsprint may have served as a site odor. (It was excluded in subsequent experiments.) Friesen (1973) had the same problem with filter paper. Since bees can even recognize the odors of individual humans (von Frisch 1967a, p. 23), the olfactory acuity and abilities of these insects cannot be lightly dismissed.

Later, Wells and Wenner (1973) again emphasized the importance of locale odors. They partially repeated von Frisch's horizontal-hive experiment (von Frisch 1967a, pp. 153-156). Two groups of foragers were trained to stations 150 m from the hive in opposite directions. As Gould, et al. (1970) and Lindauer (1971) had done, they offered different concentrations of sucrose at the two stations so that the dancing would favor one station. Since they had concluded earlier (Wenner, et al. 1969) that scent gland odor was unimportant under their conditions, no precautions were taken to control for this cue. The data are sketchy, but when the two stations offered 1.3 and 1.8 M sucrose, the number of scent gland exposures was only 10% greater at the station with the more concentrated food. Of course, the duration of scent gland exposure may also vary with food quality, but no data on this parameter were collected. Although complete records are lacking, two days' results under these conditions are incidentally presented.

The foragers collecting 1.8 M sucrose danced 253 times, while those visiting the 1.3 M station performed only 135 dances. Presumably the latter dances were also less vigorous.

Since all of the dances were on a horizontal surface with diffuse light, they were disoriented. The food odor, visitation rate, hive odor, and visual landing cues were identical at both stations; only locale odor remained to distinguish the sites. If locale odor were unimportant, recruits would be expected to arrive at the two stations in equal numbers. Instead, however, 132 recruits were captured at the 1.8 M station as opposed to only 39 at the 1.3 M site. According to Wells and Wenner, this same pattern was observed on the 9 days for which no specific data were presented.

Wells and Wenner concluded that odors -- an "asymmetry in [the] environmental cues used by recruits" -- and not dance information account for the distribution of recruits. They go on to provide a coherent outline of the locale-odor hypothesis, but refuse to commit themselves exclusively to this theory.

The locale-odor theory may also be used to explain the results of another set of von Frisch's experiments. When the forager station was so near the hive that only round dances were performed, recruits approached stations in all directions near the hive. When the Forager Station was moved far enough from the hive so that only waggle dances were performed, recruits favored stations near the Forager Station, and hence favored a general direction. The locale-odor theorists would simply infer from this that the "patch size" for which the Forager Station locale odor information was valid was approximately the size of the area around the hive for which the round dances are performed. This hypothesis gives rise to testable predictions for which present data is inadequate. It also raises the question of why the size of the round dance region should vary from one race of honey bee to another.

The Odor-Trail Hypothesis

One of the basic problems in studying honey bee recruitment is the (present) impossibility of following the flight path of individual recruits. The speed, small size, and enormous manoeuvrability of bees make

them virtually impossible to observe in flight. In fortuitous circumstances, foragers can be seen approaching a feeding station along regular paths. Recruits, on the other hand, are usually noticed only when they are nearby and flying close to the ground.

Friesen (1973) attempted to monitor the location of searching recruits indirectly through a modification of von Frisch's techniques. A group of foragers was trained to a feeding station 360 m from the hive. When the experiments began, the food odor (but not the food) was removed from the forager station. A single recruit-monitoring station with the food odor was set out somewhere in the vicinity. Recruits arriving at this station were captured and counted.

In a "fan" series, Friesen found the recruits along or slightly upwind of the (presumed) flight path of the foragers. He interpreted this as indicating that recruits use airborne forager scent trails rather than any dance information or locale odor.

In a "step" series, Friesen found recruits arriving first at stations near the forager site, and then later at stations nearer the hive. He interpreted this as refuting the theory that distance information is communicated by the dance, but could not explain the result by any odor hypothesis.

Friesen also investigated the effect of the wind. He observed that recruits arrived during or following gusts of wind. The gusts were presumed to improve the conditions for bees using positive anemotaxis as a search strategy (Farkas and Shorey 1972; Kennedy and Marsh 1974; but cf. Gillies and Wilkes 1974). Similarly, recruits found sources upwind very quickly, downwind sources less quickly, and crosswind sources only very slowly. Friesen interpreted all of his data as indicating that interactions between recruits and flight-path odors left by foragers account for recruitment. Friesen states that the wind speed was never greater than 5 m/sec, but how such odor trails would remain stable in even the slightest wind is unclear.

Later, Wenner (1974) summarized a new "population" theory of recruitment. According to Wenner, recruit bees "obtain a composite odor signal (e.g., food and locality) from the dancing bee." Then the recruit leaves

the hive and begins searching for the proper odors. The odors along the flight path serve to orient the recruits, who form a "nebulous mass in midair and downwind" of it. In addition, "the recruit pool that would develop downwind from the flight line would provide for repeated contacts among searching bees as well as between searchers and foragers." Exactly what these hypothesized interactions would accomplish is unclear. How this interpretation could explain downwind recruitment is also not obvious.

AN OBJECTIVE TEST OF THE DANCE-LANGUAGE THEORY

The honey bee dance contains both odor and symbolic location information unique to the area of the forager station. An objective test of the dance communication could be accomplished by having a dancer signal a location which it had never visited. If recruits use only odor cues, the location information in the dance is irrelevant, and they should continue to arrive in the area of the forager station. If, on the other hand, recruits use the symbolic distance and direction information in the dance, an increase in recruit arrival at the indicated location would be expected. Such a "misdirection" experiment could be done (1) by using a model bee or by causing foragers to "lie" about either (2) the direction or (3) the distance of the food. This thesis describes efforts to develop the first two approaches. The third alternative was explored by Gonçalves (1969).

Causing Foragers to "Lie" About Distance

Goncalves sought to cause returning foragers to "lie" about the distance to the food source, sending recruits to an array located further from the hive. This approach was based upon the discovery by Bisetzky (1957) that foragers forced to walk, rather than fly, to a food source would indicate a far greater distance in their dances (Fig. 16). Unfortunately, foragers are usually unwilling to walk more than about 1 m (Gary and Witherell 1971) and, upon returning to the hive, are irregular in their dancing. The distances indicated by these dances are very imprecise (Gould, unpublished), due perhaps to the irregular paths foragers take while walking. Nevertheless, returning foragers occasionally dance and do indicate distances much greater than they have walked.

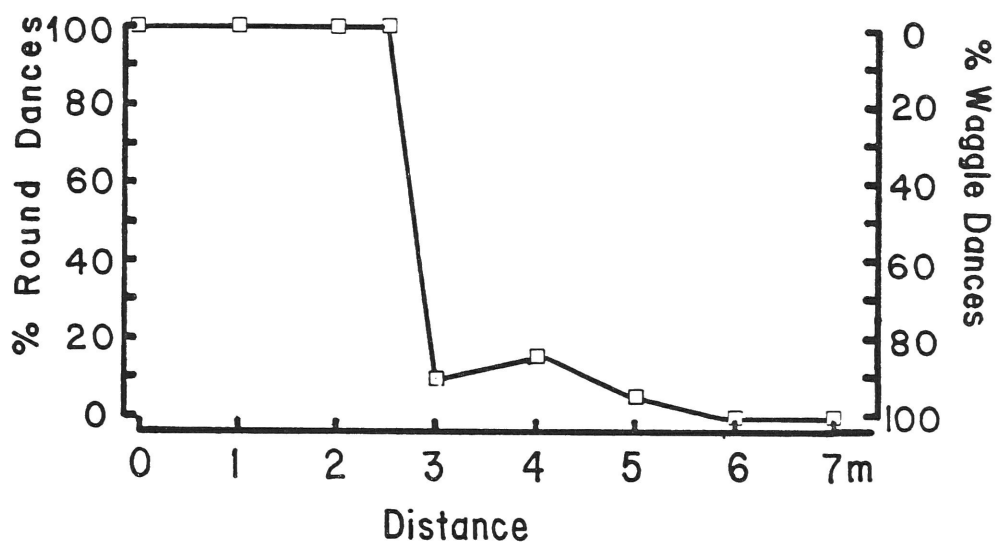


Fig. 16. Dances of Walking Italian Foragers. Foragers were trained to walk to a food source. If they danced in the hive, the type of dance (round or waggle) was recorded. Although flying foragers still perform round dances for sources at 20 m, walking foragers forsake this practice beyond 2.5 m. Dances for longer distances contain both distance and direction information.

Redrawn from Bisetzky 1957.

Although few details are presented, Gonçalves apparently trained his single forager to fly to a wooden tube 30 cm from the hive, and to walk to the food at the other end. Presumably the food was unscented. No effort was made to prevent the forager from using its scent gland, even though frequency of exposure is maximized when the food has no scent (Wells and Wenner 1971). After feeding, the forager flew directly back to the hive.

Arranged around the hive at 45° intervals were 8 stations (Fig. 17). Although in any given experiment all the stations were at the same distance from the hive, the distance used was varied in different experiments from 4 m to 40 m (in this regard see Fig. 5). From the time that the forager danced until it reentered the tube, the (presumably unscented) dishes of food at the stations were uncovered. The logic behind the manoeuver of covering and uncovering unscented solutions was not explained. The stations were made of the same wood as the tube. (Perhaps the uncharacteristic inclusion of this detail indicates that the wood had an odor.) Recruits approaching the stations were counted or, if they landed (and fewer than 10% did) they were killed. Recruits arriving at the feeding station at the end of the tube were not captured, even though they would be expected to return to the hive and dance normally.

The wind always blew from the hive toward the tube and Station A in the array. Thus the station in the same direction as the feeding site, and hence in the direction supposedly indicated by the dancing, had the odors of the hive and forager's scent gland blown toward it. Of 375 recruits, 102 arrived at the feeding station, 69 at Station A, 48 and 57 at the stations 45° to the left and right (H and B, respectively) and 89 at the remaining 5 stations.

These results may be interpreted in two ways. Either the recruits were attracted to the stations favored by the hive and scent gland odors, or the dance direction was communicated. The second possibility is unlikely since the length of the tube was rarely more than 2 m. As Figure 17 indicates for the race used in this experiment the dances should have been round dances, and hence have had no direction component whatsoever. When a 1 m tube was used, Station A was favored still more, even though the tendency against waggle dancing should have been even greater.

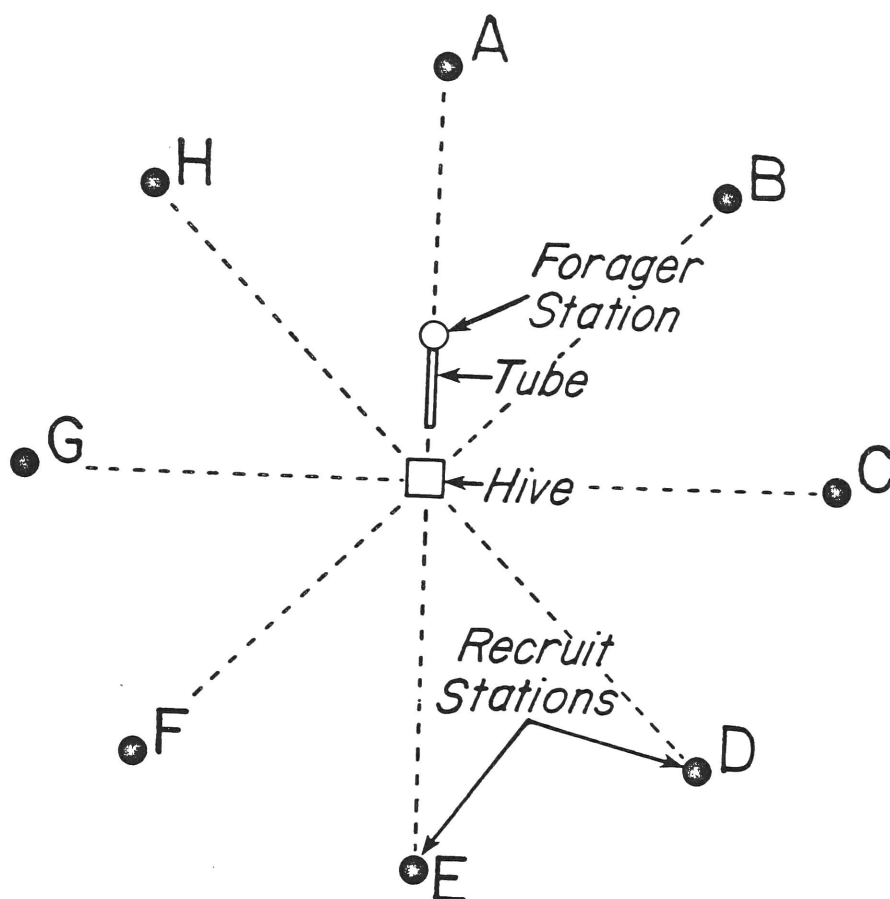


Fig. 17. The Gonçalves Array. A forager was trained in an unspecified manner on an undescribed solution to fly to a tube of varying length 30 cm from the hive, to walk through the tube to the food, and then fly directly back to the hive. Eight Recruit Stations were arranged around the hive in a circle (whose radius varied from experiment to experiment), and offered the same unspecified solution at intervals (tied, for some reason, to the current location of the forager). Recruits were seldom captured, and never at the Forager Station. The wind blew from the hive to Station A. Recruits favored the Forager Station and (to a lesser degree) Station A whether or not the tube was sufficiently long to cause the foragers to perform dances with direction (and distance) information (see text). Redrawn from Gonçalves 1969.

In two later experiments, Gonçalves increased the tube length to 3 m. As Figure 17 indicates, only at this point should some direction information appear in the dances. Indeed, it is only in these experiments that he reported even a crude dance direction. The distribution of recruits in these two experiments was identical to those obtained with the shorter tube. Since the same results were achieved both with and (presumably) without direction information in the dance, Gonçalves' conclusion that there is "communication of direction by means of dancing" seems wholly unjustified. On the whole, this technique is too inexact to be practical (Gould, unpublished data).

THE MODEL BEE

A model bee could be used to present recruits with a dance whose components are under the control of the experimenter. Provided bees respond to it as to a normal dancer, the model's odors could be made inappropriate for the location coded in the dance. The distribution of recruits in the field would indicate whether the dance information can be used. A model bee could also be used to dissect the dance communication in detail, and to learn something about how honey bees receive, process, and use the dance information.

Previous Attempts

Steche (1957) claimed to have built a successful model bee, but, to quote von Frisch (1967a, p. 104), "his data are very inexact and later repetitions were unsuccessful." Since Steche did not know about the dance's sounds (Esch 1961; Wenner 1962), it is very doubtful that his device could have worked. Since odor alone can recruit bees (von Frisch 1967a, pp. 23, 30-35, 152-153; Free 1969), great care must be taken in analyzing such experiments. For example, Lopatina and Chesnokova (1969) reported that their (undescribed) model recruited foragers back to a familiar source. Attempts to recruit new bees met with no success. Since experienced foragers typically pay little or no attention to dances with familiar odors (von Frisch 1967a, pp. 23, 30-35, 152-153, 257-264) but are recruited nonetheless, these results are not very convincing or meaningful.

Great progress toward a model bee was made by Esch (1964). Although not ultimately successful, he was able to show that it is very important for the model to provide the correct odors and sound. Esch coated his models -- dead bees or pieces of wood -- with wax, and left them in the hive to absorb its odor. (An uncoated dead bee would have been recognized as such and have been disposed of by the other bees.) The model was then attached to an (undescribed) mechanical device and made to waggle. Esch found that although bees failed to follow the model, at least they did not attack it. Esch (per. comm.) later used a small wax-coated microphone as the model. He was able to play the dance sound back through it. When the sound (described below in detail) was produced, other bees oriented to the model. Unfortunately, the model soon overheated, driving the attenders away. No bees were stimulated to fly out in search of food.

Reproducing the Shape and Waggle of the Dance

The waggle dance (Fig. 4) consists of a straight run during which the bee waggles from side to side about a point just in front of its head, followed by a rapid semicircular return to the starting point. The waggle rate is about 13 Hz. The lateral extent of the waggle is greater for more desirable food. The tempo of the dance -- the number of dance cycles per minute -- varies with the distance, while the orientation of the straight run correlates with the direction of the food.

In the experiments reported here, the model was attached to a piece of 1 mm O.D. stainless steel tubing which ran inside a 1.5 mm O.D. tube, also of stainless steel (Fig. 18). By attaching the model as shown, it waggled about a point in front of its head. The waggle was created by attaching the upper end of the narrower tube to a speaker coil through which a 13 Hz tone was played. The intensity of the signal controlled the lateral extent of the waggle. The duration of the waggle was controlled by a footswitch and a photographic darkroom timer.

Since the dancer waggles about a point in front of its head, but turns about its thorax, it was necessary to offset the tubes with a cam in order to conveniently control the model's movements (Fig. 18). The cut-out in which the cam moved caused the model to recreate the normal figure-8 pattern. The cutout could be rotated to control the direction of the dance.

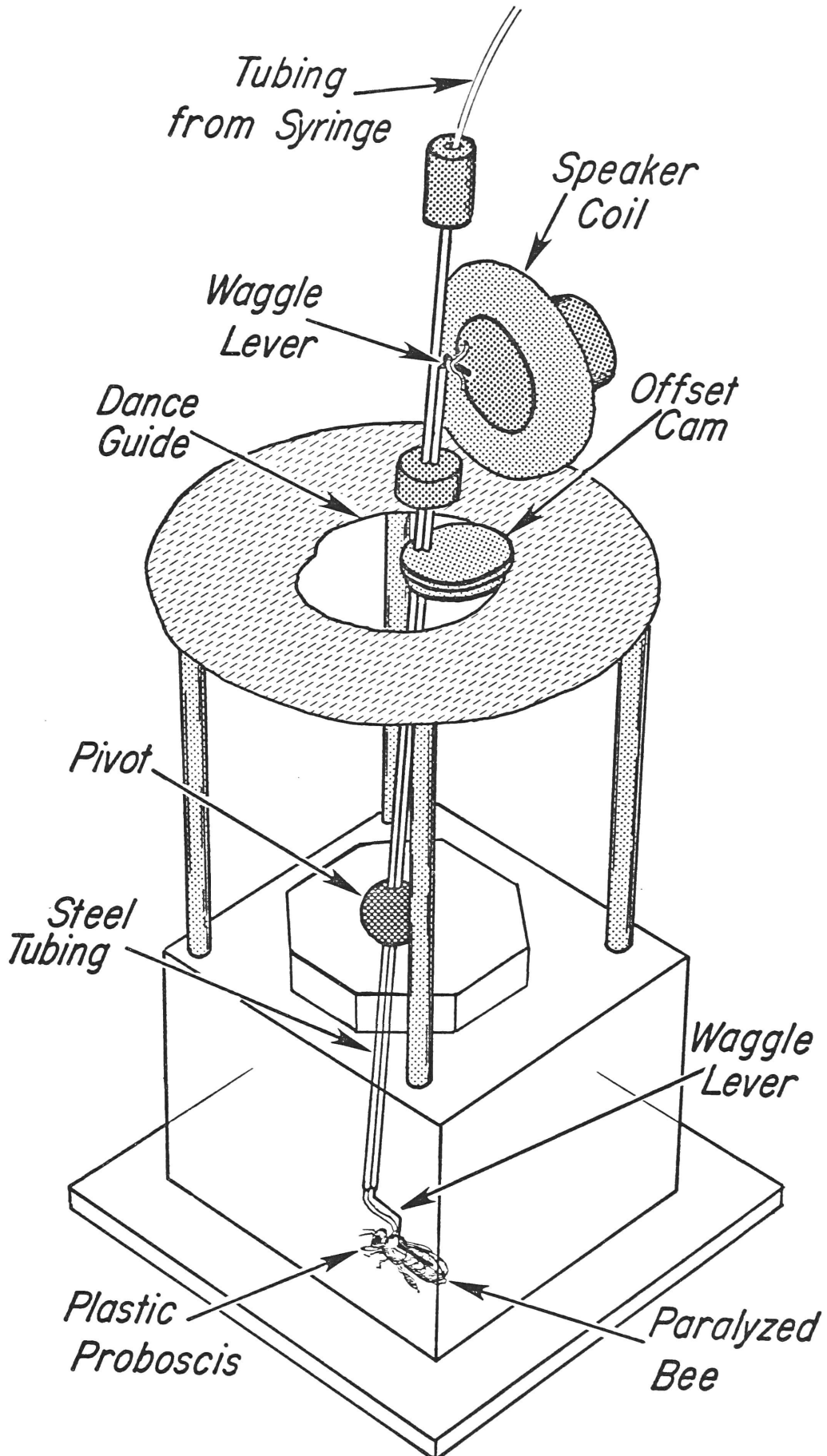


Fig. 18

Fig. 18. The Model Bee. A paralyzed bee was attached to a 1 mm rod which passed up through a larger rod to the speaker coil. The waggle frequency was played into the coil to cause the bee to vibrate. An artificial proboscis of 1 mm Intramedic plastic tubing was passed down through another tube and ended near the model's head. Tiny drops of artificial nectar were offered by attaching the upper end of the tubing to an automatic microliter syringe. The tubes passed through a pivot made from a teflon ball. The model was guided manually along the dance guide. The offset cam allowed the model to vibrate about a point in front of its head, and yet turn about its thorax. The device was attached to the side of an observation hive. A small trap door was opened to give the model access to the bees.

Reproducing the Smells and Tastes of the Dance

Dancers regularly distribute food samples to dance followers. The overwhelming majority of recruit bees arriving at a station have had one of these samples (Dirschedl 1960). This "reinforcement" may well be crucial in stimulating recruits to fly out in search of the food. In order to provide this cue, the model was equipped with an artificial proboscis: a piece of # PE 50 Intramedic tubing was passed down the other section of 1.5 mm tubing (Fig. 18). The tubing ended near the head of the model. The other end of the tubing was connected to an automatic syringe. Food samples were dispensed in tiny alloquats by pushing a button on the syringe.

The first model was a piece of wax-coated wood of about the size and shape of a bee. After it had been left in the colony for several days to absorb hive odor, the model was no longer treated as a piece of debris by the bees. Unfortunately, the wooden model was not the subject of begging by its hivemates. Free (1956) found that starving bees would beg from models with wire antennae. When wire antennae of the same size were attached to the wooden model, virtually no increase in begging occurred. Perhaps the bees were not sufficiently starved, even though the hive was kept hungry.

As an alternative to the wooden model, a bee was paralyzed with .01 ml of curare (McCann 1966). Injections had to be made carefully into the abdomen since the crop can be easily punctured. When this happens, the contents appear on the abdomen and are consumed by other bees. Injections of curare into the thorax have little or no effect.

When a curarized bee is placed among other bees, it is frequently the object of begging. When the paralyzed bee was attached to the model device and the intramedic tubing positioned to end near the bee's head, begging bees accepted the food offered. When larger diameters of intramedic tubing were used, more than one bee would feed at once.

In general, the paralyzed bee was received in a more nearly normal fashion than was the wooden model. Several difficulties arose in attaching the bee to the device. Various glues provided a strong bond, but the

glue-associated odors obviously upset nearby bees. A drop of hot wax provided a less secure but a more olfactorially unobtrusive attachment. A better method, when possible, was to tie the wax-attached bee to the device with fine wire or thread.

Reproducing the Dance Sound

The dance sound is produced by the flight muscles of the thorax (Simpson 1964). Since the wings remain folded, no flight occurs. The indirect flight muscles -- which provide almost all the power for flight -- are myogenic with a natural frequency of 200-350 Hz (depending on loading) (Dade 1962; Esch 1964; Esch and Wilson 1967). The basic frequency of the dance sound is 250-280 Hz (Esch 1961; Wenner 1962a, 1964), while that of the stop signal is about 330 Hz (measured from Esch 1964). The dance sound is composed of the 250-280 Hz vibrations pulsed on and off at about 30 Hz. The dance sound is crucial to recruitment. Esch (1967) found that none of the 15,000 silent dances he observed ever resulted in recruitment.

Hearing through the legs

Bees are known to detect vibration with the subgenual organs of their legs (Autrum and Schneider 1948). The "freezing" response, for example, is known to be mediated by these organs (Little 1962). Indeed, the behavioral audiogram of the response (Fig. 19) approximates the neurophysiological results of Autrum and Schneider (1948, also plotted in Fig. 19). The crude audiogram of Frings and Little (1957) showed a peak response at 600-800 Hz. In their experiment the sound was played into the air from a speaker, and was assumed to be vibrating the comb. Since the resonance properties of the comb would largely determine the degree of loading of the airborne sounds into the comb, their measurements may say more about the response of honey comb than honey bees. (In fact, comb does resonate at 600-850 Hz depending on its contents.) The peak sensitivity of the subgenual organ corresponds to the frequencies used in the "tooting" and "piping" between unemerged virgins and the old queen preparing to leave with the swarm (Wenner 1962b). The queens load the sound into the substrate by pressing their thoraxes against the comb. Again, the vibrations are produced by the indirect flight muscles (Simpson 1964; Wenner 1965).

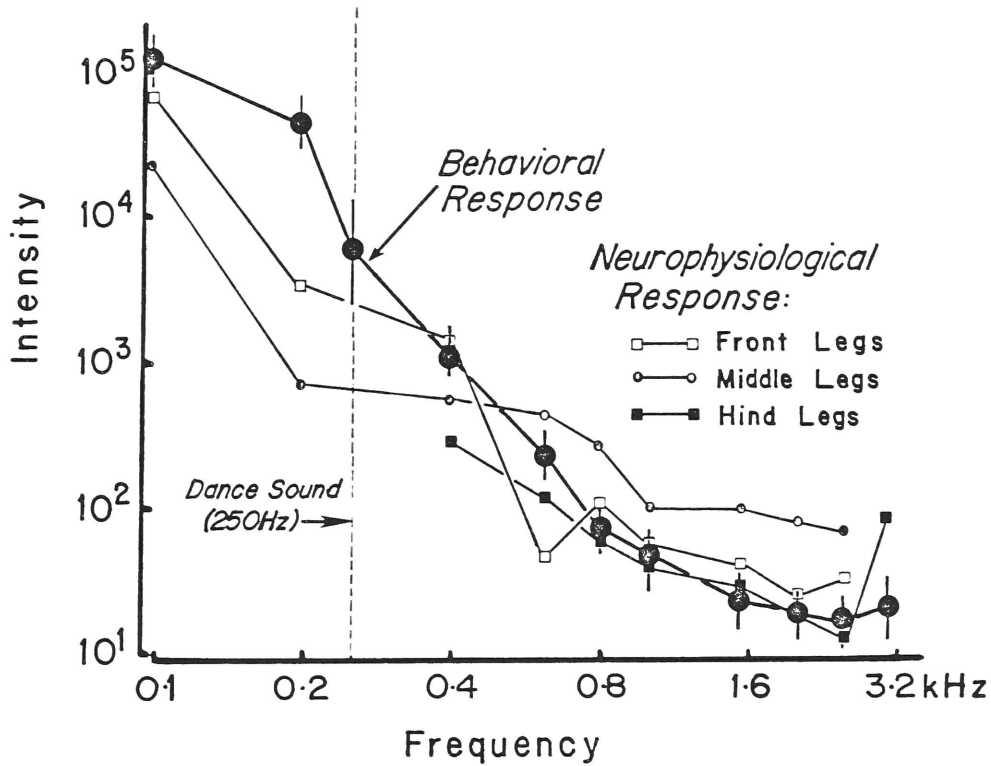


Fig. 19. Response of the Subgenual Organ. The behavioral data was obtained by varying the amount of substrate vibration until a defined threshold freezing response was obtained. The amount of sound was measured by an accelerometer attached to the substrate (see text). The neurophysiological results (based on data in Autrum and Schneider [1948]) represent the amount of vibration necessary to obtain a defined response from the subgenual organ. In both cases, the lowest point of the graph (and therefore the area of greatest sensitivity) is within the region of the queen sounds, while the threshold is much higher at the frequency of the dance sound.

These exchanges between queens, which may serve to assure the presence of a new queen while preventing a fight between the old and new queens, elicit the freezing response. Since the comb is constantly vibrating with the buzzing and other activities of tens of thousands of workers, the freezing response may serve to reduce the background noise during queen communication.

Although many reviewers feel that bees must also detect the dance sound through the comb with their subgenual organs (e.g., Wilson 1971; Michener 1974; Schwartzkopff 1974; Michelsen and Nocke 1974; etc.), there is actually no evidence that they do so. Since the dancers do not press their thoraxes against the comb, any loading of the sound into the comb must be done through their thin, constantly moving legs. The sensitivity of the subgenual organ is very low at the frequencies of the dance sound -- as much as 25 dB down from the sensitivity at 3 kHz (Fig. 19). Acoustic isolation of different but adjacent dances and stop signals would be difficult if the sound were transmitted through the substrate. Since the dance is only attractive when the sound is included (Esch 1964), it would be difficult to explain the effectiveness of swarm dances because the substrate in this case consists of the loosely packed bodies of other bees. It would also be difficult to account for the attractiveness of the occasional dances in observation hives in which the forager dances on the glass, while the attenders follow on the (acoustically isolated) comb. Nevertheless, since the alternatives (discussed below) seem nearly as unlikely, an attempt was made to test the theory that the dance sound is transmitted through the comb and is detected by the subgenual organs.

Sound vibrations were loaded into the substrate with a Sound Reproducer # 21 F 01590 (Lafayette Radio Electronics, Syosset, L.I., N.Y.). The hive was constructed so that dancing occurred only on one side of the bottom frame. The foundation used in this comb was wax-coated plastic (Dadant and Sons, Hamilton, Illinois). Since bees cannot chew through the plastic, it was possible to leave the other side exposed. This arrangement, however, allows the bottom frame to become chilled unless a heating pad is kept on the exposed side. The sounds were loaded directly into the foundation and monitored by a B&K type 4333 accelerometer.

Pure tones were generated by a Krohn-Hite 400c Oscillator, amplified by a Dynaco SCA 800 amplifier and transmitted by the sound reproducer. The freezing response was elicited by adjusting the amplifier gain until either dancing bees over the entire frame stopped moving -- a rather crude index -- or until returning bees froze immediately upon landing in the flight funnel. The accelerometer was attached to the comb foundation or the funnel 10 cm from the sound reproducer. The output of the accelerometer was displayed on a Tektronics type 502 oscilloscope and the freezing threshold intensity recorded for a variety of frequencies. Figure 19 shows these values (corrected for the frequency response of the accelerometer). The results approximate the values measured by Autrum and Schneider (1948).

The queen sounds, which also cause the workers to freeze, have a pulsed structure (Hansson 1945; Wenner 1962b). These sounds were synthesized and recorded using the Krohn-Hite 400c Oscillator, a General Radio Tone Burst Generator, and a small cassette recorder. When the queen pulses were played into the comb they had to be approximately 4 dB louder than the unpulsed tones to achieve the same response. The queen, however, who had ignored the pure tones, responded to the pulses on 12 of 21 trials. By using the same pulse timing, different carrier frequencies were used (e.g., 500 Hz, 1 kHz, 1.5 kHz, 2.5 kHz). As with the freezing response, far greater intensities were required with the lower frequencies.

In the same way, the stop signal -- a 330 Hz tone of 1/4 sec duration -- was played into the comb foundation under or near active dances. No available intensity was sufficient to stop the dances more often than would be expected by chance alone. A 330 Hz pure tone, on the other hand, froze both dancers and attenders instantly.

Hearing with the antennae

Many insects are able to detect and localize vibrations with their antennae. For example, the antennae of Drosophila females are used to detect the courtship songs which the males produce by vibrating their wings (Manning 1967). A male mosquito can locate females in midair on the basis of the sounds they produce (reviewed by Belton 1974). In each of these cases, the ability is mediated by Johnston's organ, which is located in an articulation of the antennae. Many insects also use this organ to detect their own flight movements (reviewed by Gewecke 1974).

In order for the bees to hear, their antennae must move with respect to their heads. The antennae of the honey bee (Fig. 20) consist of two parts. The proximal portion is called the scape, while the distal portion is known as the flagellum. Johnston's organ is found at the base of the flagellum (see de Wilde 1941). Campaniform organs, shown by Pringle (1938) to be proprioceptors, are located at the base of the antenna. Hence, the movement of the proximal part of the antennae may be monitored separately.

The response of the organs depends (we suppose) on the resonance of the portion of the antenna to which it is attached (Fig. 21). It is striking that the peak resonance of the flagellum is at about 280 Hz -- the frequency of the dance sound. It is also intriguing that the resonance of the whole antenna is at or below 20 Hz -- very close to the 13 Hz of the dance's waggle.

Bees do not freeze in response to airborne sounds, and this has been taken to mean that they are deaf to such vibrations. Since the antennae do not mediate the freezing response, however, the "deafness" of bees to airborne sounds may not be real. Proximity to the sound source may also be important. Since the sound source -- the bee's thorax, for example -- has a finite size, there is a "near-field" region in which the intensity loss due to spreading is very small. In this region -- one or two source diameters -- the sound at the receiver is effectively coming from an extended plane source, and hence is subject to very little spreading loss. At larger distances the loss is more nearly that which is typical of point sources -- the sound intensity falls off as the square of the distance. In the near field, therefore, sound intensities may be very high indeed. For example, assuming the thorax to be a perfect sphere and the only sound source, Esch's (1964) measurement of 74 phon would be 14 dB higher at the thorax, and 8 dB higher 2.5 mm away. To a human ear 30 cm away the sound level would be below 10 phon -- inaudible due to the masking noise produced by the thousands of other bees in the hive. (Phons are dB psychophysically weighted to the frequency response of the human ear.)

Esch (1964) showed that the dance sound could be detected as a vibration superimposed on the waggle. Since dance followers keep their

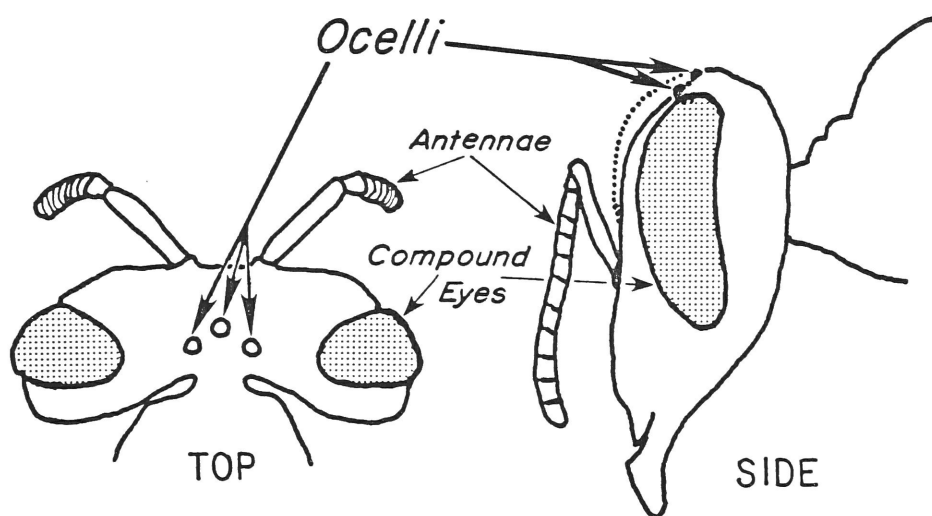


Fig. 20. The Head of the Honey Bee. The three ocelli are located on top of the head as shown. The antennae are attached to the front of the head, between the compound eyes. The single proximal portion is the scape, while the segmented, distal part is the flagellum. The flagellum bears the olfactory receptors. Redrawn from Snodgrass 1956.

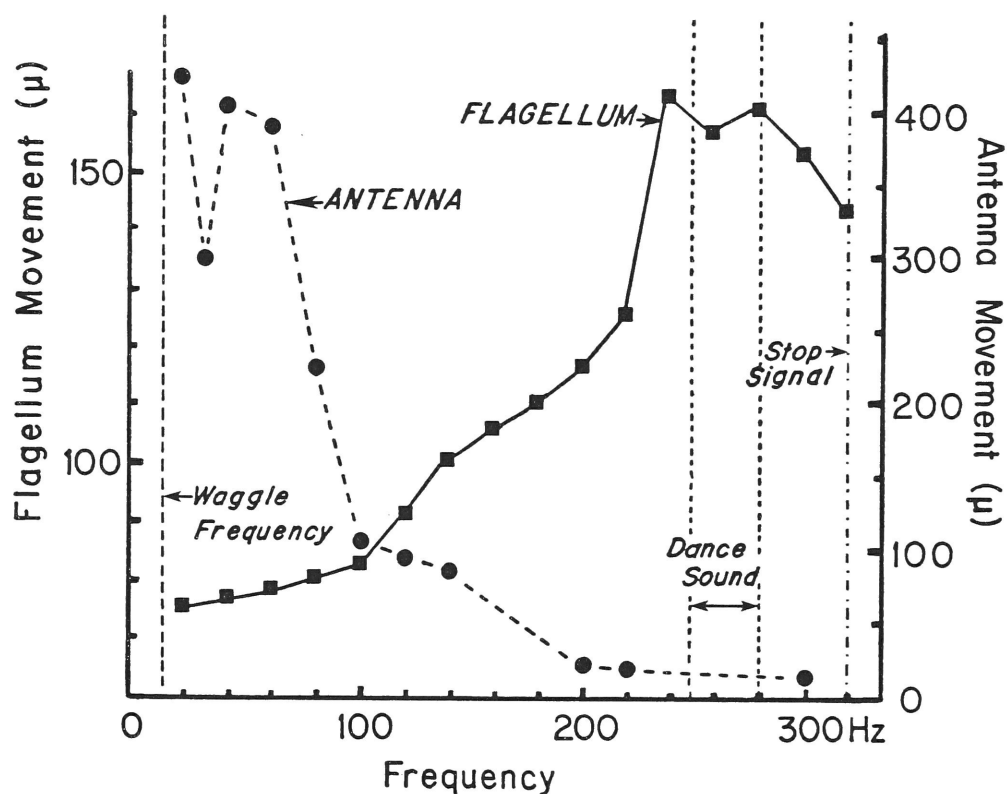


Fig. 21. Resonances of the Antenna. The resonance of the whole antenna is at or below 20 Hz. The waggle frequency is 13 Hz. The resonance of the flagellum is near the frequency of the dance sound -- 250-280 Hz. The antenna may be a two-channel mechanical filter.

Redrawn from Heran 1959.

antennae in contact with the dancer's abdomen, the sound might be perceived by direct touch. Such an explanation, however, does not account for the detection of the stop signal. The dancer certainly is not in antennal contact with the followers producing these sounds.

Nevertheless, an attempt was made by this writer to communicate by adding the sound to the waggle. The waggle and dance-sound signals were mixed and fed into the waggle coil. Even when the dance-sound vibrations were visible (as they never are in a real dance) the bees showed no additional interest in the model.

Another possibility would be to produce a very loud dance sound near the model. The difficulty with this approach is simply making the sound loud enough and near enough. When the sound was played back through a B&K 1/2" probe Microphone (type 4133) the intensity was much too low. A small earphone was also not nearly powerful enough. Louder devices are too large to be used with the present arrangement.

Another approach, still being developed, is to cause the paralyzed bee to make the sounds itself. Since the indirect flight muscles are myogenic and very large, it is possible to place electrodes in them and cause them to vibrate at the proper frequency. Very fine insect pins insulated to the tip were used as electrodes. Two Tektronix 101's and 163's were used to produce the stimulation pulses, although the frequency and duration of the shocks were not critical. Although the stimulated bees vibrated their folded wings at 250-300 Hz, no sound was produced. Some other element must be involved in the production of honey bee sound.

As Boettiger and Furshpan (1952) found, flies produce audible "clicks" as their indirect flight muscles move. This click disappears under ether anaesthesia, but remains with CCl_4 . The sound is produced even if the wings are folded (Esch and Wilson 1967; Ewing and Bennet-Clark 1968). A small muscle in the thorax, musculus latus, must be contracted in order for the sound to be produced (Nachtigall 1974). Under CCl_4 anaesthesia, honey bees also produce a click when the thorax is squeezed dorso-ventrally. The click disappears under ether or curare. Whether the sound will be produced when the indirect flight muscles are stimulated under CCl_4 anaesthesia is being investigated. Unfortunately, the odor of

CCl_4 is offensive to bees. Models exuding this odor are avoided by other bees. Other methods of administering the CCl_4 and chemical substitutes are being investigated. Ultimately, it should be possible to test the possibility that the click might be the important part of the dance sound. This line of work is being actively pursued.

CAUSING FORAGERS TO "LIE" ABOUT DIRECTION

If foragers could be caused to reliably "lie" about the direction of a food source, the dance-language theory could be objectively tested. Although the odors carried back to the hive as well as those left in the field would specify the actual feeding site, the symbolic component of the dance would specify a different location. The distribution of recruit arrivals in the field would reveal whether the symbolic information in the dance is communicated and used. As mentioned earlier, to cause foragers to misdirect recruits requires that the parameter to which the forager orients the direction of its dance be different from that to which the recruits orient.

Bees normally orient their dancing and dance interpreting with reference to gravity. "Up" is taken to be the direction of the sun and the angle of the dance from vertical the angle between the food and the sun (as seen from the hive). When dances are performed on a vertical surface in the open -- on the side of a swarm cluster, for example -- they are oriented instead with respect to the sun's actual position, if it is visible, or with respect to a compromise between gravity and the position of the sun inferred from the sky's polarization pattern, if it is not (von Frisch 1949, 1950). Similarly, if the intensity of the sun is decreased, the degree of dance reorientation from light to gravity decreases (von Frisch 1948, 1962; Edrich 1972). Of course, both foragers and recruits are similarly reoriented, so that no misdirection occurs (von Frisch and Lindauer 1961).

When the ocelli (Fig. 20) of workers are covered, bees become far less sensitive to light (Lindauer and Schricker 1963; Schricker 1965). Bees with painted ocelli need higher light levels to forage -- they fly out later in the day and return earlier in the evening (Fig. 22). Bees

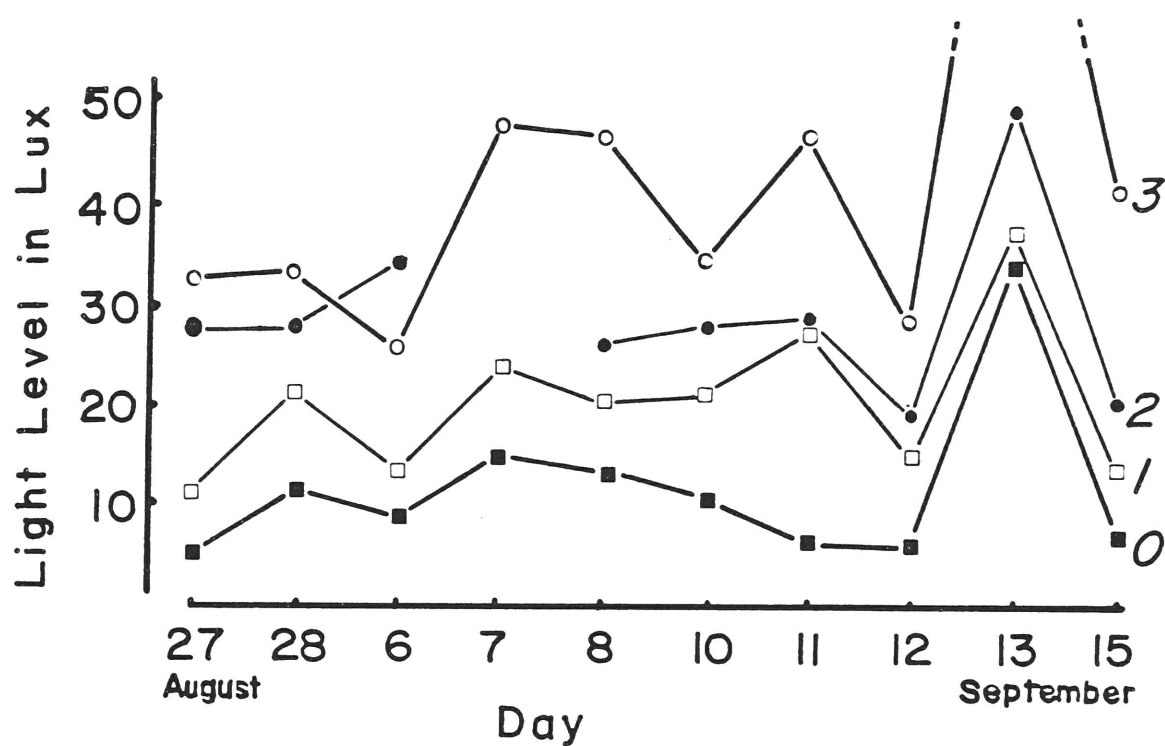


Fig. 22. Minimum Light Levels for Forager Flight. The ambient light level when foragers ceased flying was measured over a period of three weeks for bees with various numbers of ocelli covered. Bees with no ocelli covered (curve "0") required less light to continue to forage than bees with 3 ocelli covered (curve "3").

Redrawn from Lindauer and Schricker 1963.

with painted ocelli also need a brighter light in order to display phototaxis (Fig. 23) and require greater intensity differences to reliably choose the brighter of two lights (Schricker 1965). Oddly enough, foragers with covered ocelli tend to drag their third pair of legs (Götze 1927; Goodman 1970).

Although light will cause foragers with painted ocelli to reorient their dances, the source must be considerably more intense than that needed to reorient untreated bees (Fig. 24). If the intensity of the light is adjusted to an appropriate intermediate level, the dances of untreated bees can be completely reoriented without altering the dances of foragers with covered ocelli. Hence, if the dance-language information is used, untreated attenders would interpret the dance direction with regard to the light, while the painted foragers would be orienting their dances with regard to gravity. For example, if the food source were in the direction of the sun, the dances of foragers with covered ocelli would point "up" -- the direction assigned to the sun. Untreated recruits, however, would orient with respect to the light. If the light were shining on the dancing area from 90° to the left of vertical, then the upward-directed dances would be interpreted as indicating a location 90° to the right of the sun. Recruits would be expected to search for the food at the wrong spot if the dance language is used, whereas the position of the light should be wholly without effect if it is not.

PROTOCOL

Training

Initially, two groups of foragers were trained using Gary's methods (personal comm.; Gary and Witherell 1971). A 10 cm-wide board extended 2 m from the hive entrance and flight funnel. Drops of 2 M orange-scented (25 1/1) sucrose were first placed in the funnel. These drops were discovered accidentally by bees going in and out of the hive. Soon a small group of foragers were making regular trips to these drops. One of the feeding devices used throughout this work (Fig. 25; based on a design of Renner [1959]) was placed on the board close to the hive. Several lines of tiny drops of the sucrose solution were "drawn" to lead the bees from the

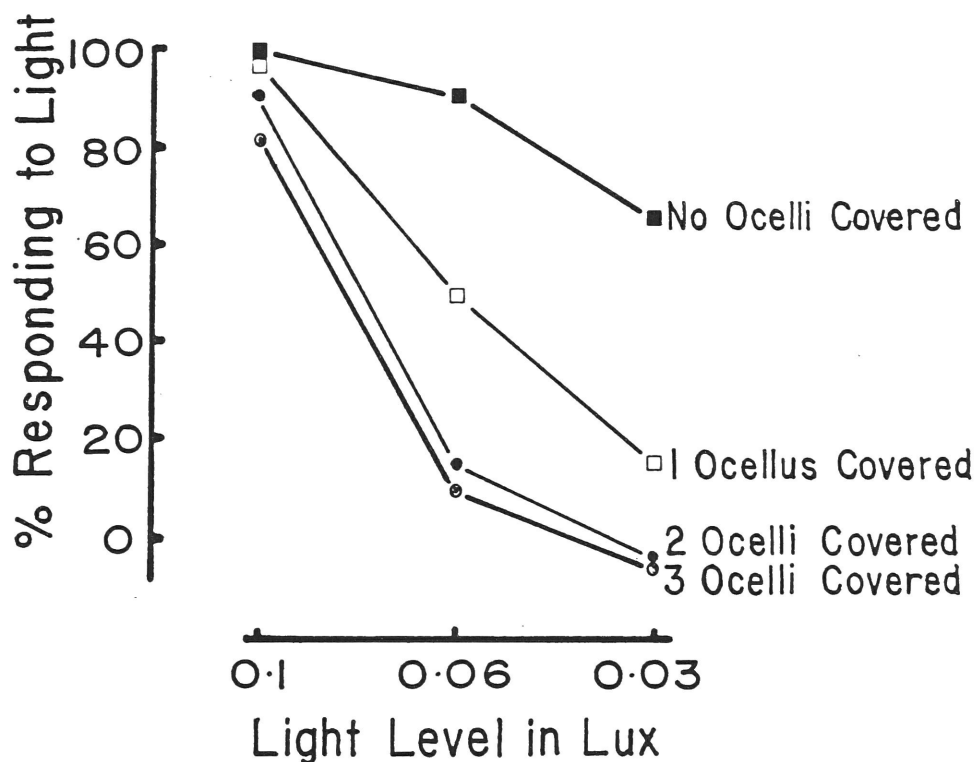


Fig. 23. Minimum Light Levels for Phototaxis. Bees with various numbers of ocelli covered were presented with a light of variable brightness. When the light level was high enough, nearly all the bees displayed positive phototaxis. At lower light levels, however, bees with covered ocelli were much less responsive. Although these data are not shown, presumably no bees -- whether or not the ocelli were covered -- displayed phototaxis when the light level was too low.

Redrawn from Schricker 1965.

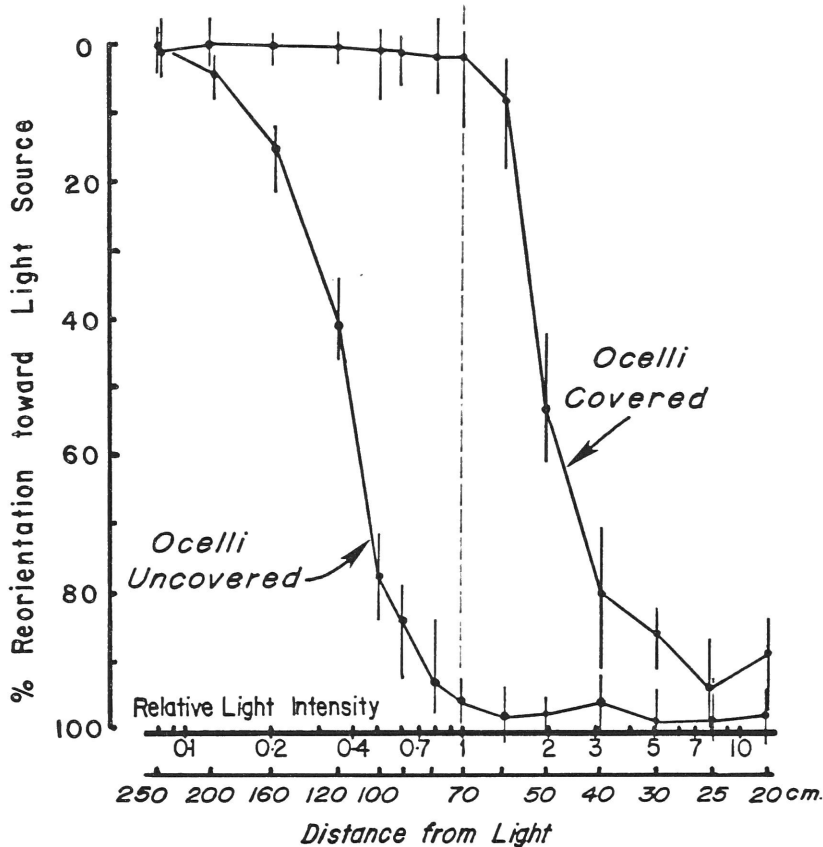


Fig. 24. Dance Reorientation to an Artificial Sun. The dance orientations of foragers were unaffected by a distant light source. When the source was moved closer, thereby increasing its apparent brightness, the dance directions shifted until they were oriented completely with respect to the light rather than to gravity. Further increases in brightness were without effect. Bees whose ocelli had been covered also reoriented their dances, but only when the light was much brighter. At an intermediate level (dashed line) the dances of normal bees were completely reoriented, while those of the ocelli-painted foragers were unaffected. Virtually all bees in each group reoriented to the same degree (the bars indicate individual scatter about the average). About 20 dances were measured for each point.

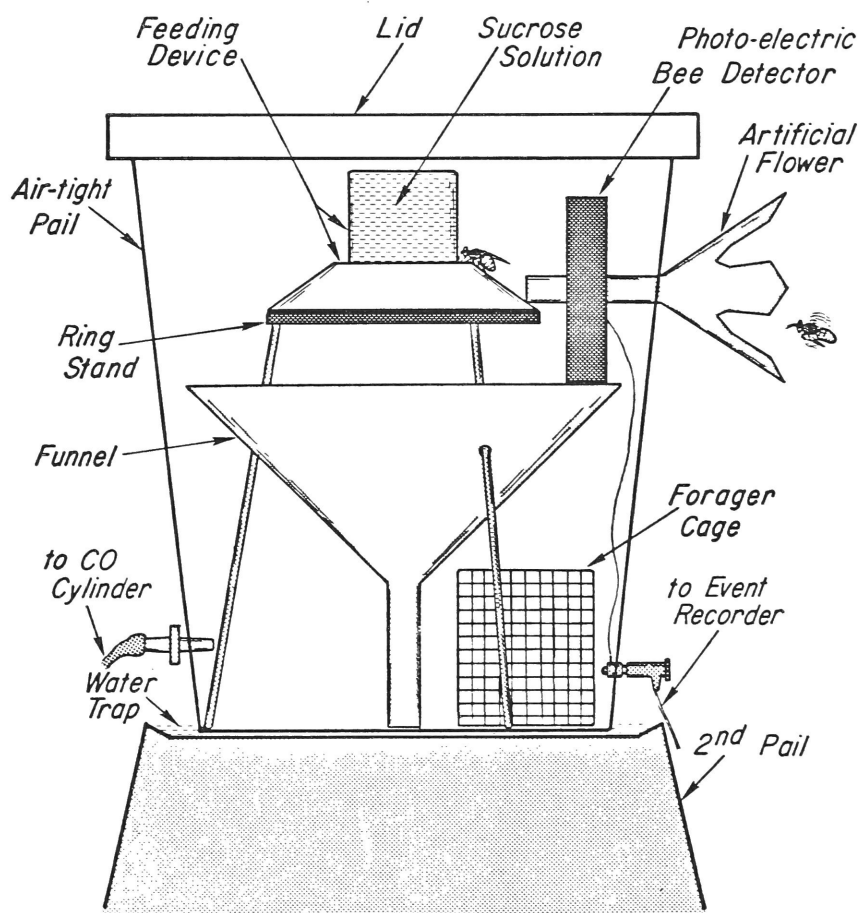


Fig. 25



Fig. 25. A Recruit Station. The station was constructed from an air-tight plastic pail. A decoy bee was placed in the artificial flower to induce landing. The "flower," fashioned from a plastic funnel, was painted to appear dark in the center and light on the edge under UV light. A wire cage of anaesthetized foragers located in the station served as an olfactory lure. When a recruit entered a station, it interrupted a beam of red light, causing a photo-electric circuit to signal an event recorder, thereby registering the arrival. As the bee continued in, it came upon a feeding device offering a sucrose solution with the experimental scent. The station was filled with CO so that while the recruit fed, it became anaesthetized and tumbled off the inclined feeding device into a funnel. The order of recruit arrivals was preserved in the linear arrangement of anaesthetized bees in the neck of the funnel. The stations stood on the water-filled bottoms of larger pails. The water helped to prevent ants from entering the stations. The pails were about 40 cm tall.

funnel to the feeding grooves. As the number of foragers increased, the device was moved gradually out along the board until bees began flying instead of walking to the food. The feeding device was then placed on a table which was moved gradually away from the hive at a rate of about 1/3 of the distance between the table and hive every 10 minutes.

At about 10 m, the solution was changed to 0.5 M orange-scented sucrose, and a second table was added. The bees were individually marked with numbered plastic tags (Chr. Graze K.G., Württemberg, Germany). The two forager stations were gradually separated. About 15 bees were allowed to frequent one table -- later the Control Station -- while at least 45-50 foragers were kept with the other. The ocelli of bees visiting the latter table -- which later became the Forager Station -- were covered with black enamel. Because of the low concentration of the sucrose solutions, foragers rarely danced and almost no new, unmarked recruits appeared. (On some days it was necessary to reduce the molarity of the feeding solution further to maintain this condition. Excess foragers were captured.) Any recruits which did arrive were either marked and incorporated into the foraging group, or were captured without the release of alarm odor by the method of Gould, et al. (1970). This technique involves placing a plastic bag over the feeding newcomer. The bee invariably stops feeding and walks up the inside of the bag, whereupon it is trapped and sealed in.

Training proceeded to the final locations for the stations. The food at the Control Station was gradually switched to 0.5 M anise-scented (25 μ l/l) sucrose. The forager dish was switched from the training table to a station similar to those described later. On subsequent days the Control and Forager Stations were simply set out at their previous locations with 1.0 M sucrose solutions, anise scented in the case of the Control Station and orange scented at the Forager Stations. When the foraging groups had reassembled -- usually within 20 minutes -- the concentration of the control solution was reduced to 0.5 M. At the Forager Station enough new recruits were incorporated into the forager group to raise the number again to 45, and then the solution was changed to 0.5 M orange-scented sucrose. If the Control and Forager Stations were to be placed at new locations, they were gradually moved at this point. Special care had to be taken at the first, since bees become "attached" to locations (von Frisch 1967a, pp. 331-333; 339-347).

Before the experiment began, 30 or more of the foragers visiting the Forager Station were captured, anaesthetized with CO, and put into wire cages in groups of 5. As described below, these foragers were used to odor bait the Experimental Stations. The scent at the Forager Station was then gradually switched to that day's experimental odor. As the experiment began, the concentration of the anise-scented solution at the Control Station was raised to 0.75-1.0 M to release a small amount of dancing. The dance orientations of the control foragers were used to confirm that untreated bees in the hive were being reoriented by the light. At the same time, the concentration of the Forager Station solution with the experimental scent was raised to 2.0 M to release vigorous dancing. When the experiments ended, the food was removed.

The Artificial Sun

A 650 w quartz "movielite" (# 15 E 68005 from Lafayette Radio Electronics) was used to reorient the untreated bees. Although honey bees are more sensitive to UV than to any other part of the spectrum (Autrum and Zwehl 1964), and although UV light is required by bees to orient to polarized light (von Frisch 1967a, pp. 401-403), longer wavelengths are effective in orientation to an artificial sun (von Frisch 1948). Quartz light sources are rich in the UV, but the plexiglas which covered the observation hive absorbed much of this energy. At 350 nm 90% of the UV was passed, while at 330 nm only 10% was transmitted. The peak of sensitivity in the UV is at 340 nm for the bee (Autrum and Zwehl 1964).

The quartz lamp also produced a significant amount of IR -- enough to melt the comb if precautions were not taken. To remove the IR portion of the spectrum -- to which bees are blind -- a piece of heat-absorbing glass (# 4072 from Edmund Scientific Co., Barrington, N.J.) was placed over the light. The glass was held between two pieces of asbestos wire gauze which also served as a mask, confining the light beam to one part of the comb. This arrangement is pictured in Figure 26.

When the light was first turned on, the bees often seemed disturbed. Previously inactive bees would begin to run about, while returning foragers would go to the considerable trouble of moving to the dark side of the hive



Fig. 26. The Artificial Sun. A quartz movie light was moved to the appropriate distance and angle from the dancing. A heat-absorbing filter removed enough of the IR to prevent the hive from overheating. A video tape record of the dancing was made for later analysis.

to dance. After about 15 minutes, however, things returned to normal. In each of the experiments the light was left on for 30 minutes before beginning in order to adapt the bees to its presence. During this period the light was in the "up" position -- that is, shining on the dancing bees from the direction away from gravity. Since this is the direction normally assigned to the sun in a dark hive, no reorientation of untreated bees or of the dances of control foragers took place. When the experiment began, the light was moved to the appropriate angle with respect to the dance area.

Dancing took place almost exclusively on the upper right quadrant of the bottom frame -- an area measuring about 5 cm in diameter. The concentration of the dances into this area was a consequence of the bees' failure ever to build the comb on the bottom third of the frame. Figure 27 shows the distribution of 100 dances. Since the artificial sun was a finite distance away, a certain amount of parallax error was unavoidable (Fig. 28). This error limits any accuracy measurements made using the misdirection technique.

The distance from the light to the hive was varied until the dances of the untreated control foragers were completely reoriented while those of the ocelli-painted bees were not. Occasionally the dances of a particular treated forager would show some degree of reorientation to the light -- probably indicating incomplete covering of the ocelli. Such bees were always captured. The appropriate distance between the light and the hive varied slightly according to the time of day and cloud cover. No quantitative data were collected on this point.

Recording the Dancing

A Sony Videocorder DV 2400 with a 10 mm lens (Fig. 26) recorded the dancing in the hive. A digital clock (# GC-1005 Heathkit, Benton Harbor, Michigan) and two-channel thermometer (Heathkit # ID-1390) were located in the bottom of the camera's field of view. In this way the time to the nearest second as well as both the wet- and dry-bulb temperature readings were continuously recorded. The video tape was changed as necessary.

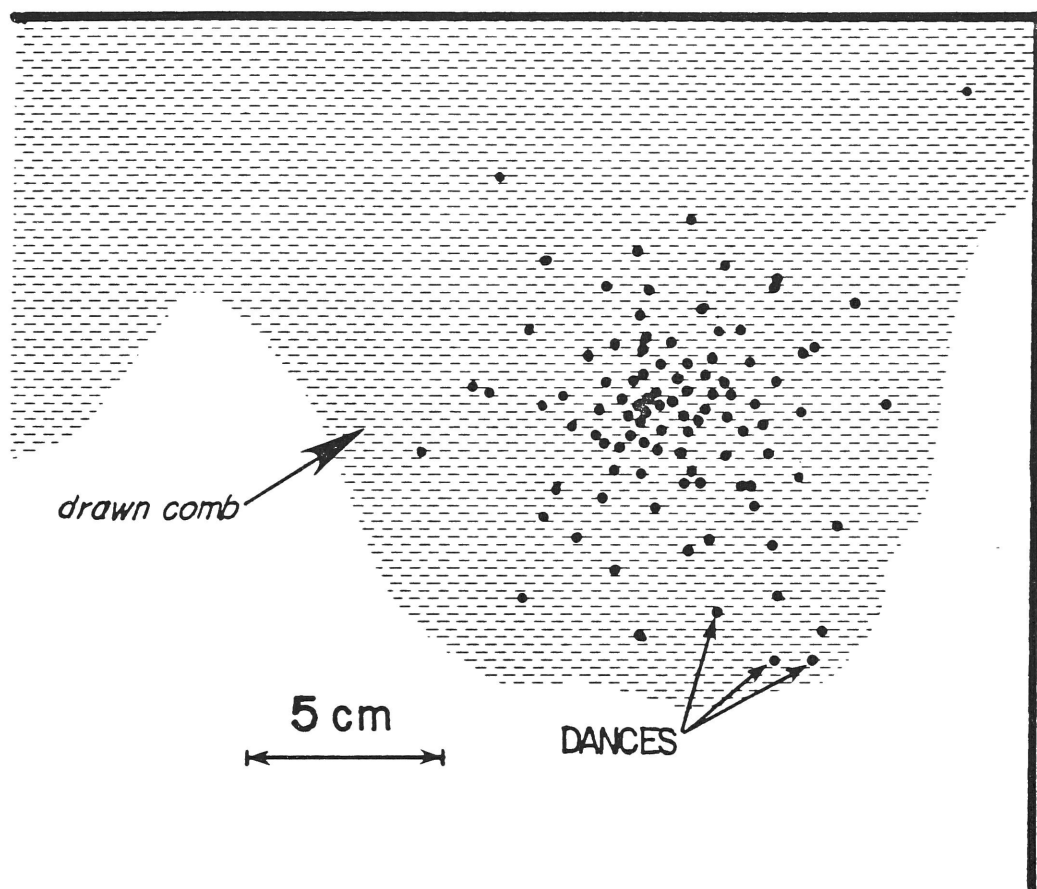


Fig. 27. Distribution of Dancing on the Comb. The colony never fully built the bottom comb, probably because the other side was exposed and hence was too cold for raising brood. As a result, dancing was confined to the upper half of the end near the entrance. Each dot represents the approximate center of a new dance. The figure depicts the locations of 100 dances during a 3° direction array experiment.

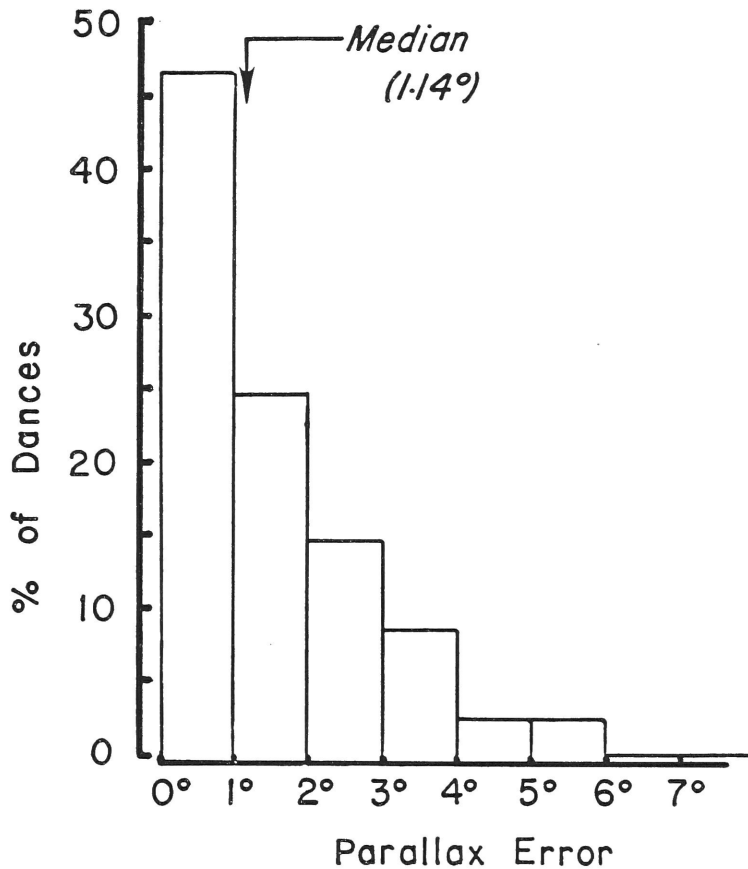


Fig. 28. Parallax Error for Dance Attenders. Since the light was a finite distance from the hive, and since not all bees danced on the same spot, a certain amount of parallax error was inherent in the experiment. The dance locations of 500 dances from a 3° direction array experiment were measured and the results plotted. The median error was only 1.14°.

The Artificial Flowers

When searching recruits arrive in the field, they must find the appropriate olfactory and visual cues in order to land and be recorded. Recruits must be captured so that they will neither be counted more than once, nor return to the hive and dance. Recruits are usually captured manually. Unfortunately this procedure requires adding unusual visual and olfactory cues -- people -- to the environment. In addition, it involves considerable expense, particularly when staff benefits are included. A less expensive, less obtrusive, automatic system to attract, capture, and count the recruits was desirable.

The stations used in these experiments are elaborations of one designed by Renner (1959). His stations used a flower painted on a metal box to attract the foragers. Entering and leaving foragers passed through a beam of light, thereby triggering an electric eye. My stations displayed a flower (Fig. 25) cut from a plastic funnel and painted to conform to the pattern which spontaneously attracts bees (Free 1970). Since new recruits are often reluctant to land unless they see another bee already there, the body of an alcohol-extracted, sun-dried bee was attached to the funnel.

Inside the station (Fig. 25) a wire box containing at least 6 anaesthetized, ocelli-painted foragers provided hive odor to lure hesitant recruits. A feeder containing the experimental solution and scent was placed on a tripod, level with the flower entrance. Entering recruits passed through a beam of red light, triggering a mark on a 6-channel event recorder located in the hive shed. From the marks, the arrival times of recruits to stations at six different locations could be determined.

Care had to be taken in setting the gains on the electric-eye amplifiers in each station. Each circuit was affected by the amount of cable (22 AWG from Belden, Chicago, Ill.) leading to the recorder, the amount of ambient light diffusing into the station, and the angle of the flower funnel with respect to the sun. The tubes through which the recruits walked from the flower to the food had to be painted flat black.

A dead bee mounted at the end of a wire was moved in and out of the flower in order to set the sensitivity of each station. All flowers were pointed at least 120° away from the sun.

In order to prevent recruits from returning to the hive and dancing, they were anaesthetized with CO while feeding. The stations -- constructed from air-tight plastic pails -- were filled with CO until the decoy foragers in the wire box became quiet. A small container of CO was attached to each station, providing a slight flow to replace the gas lost through diffusion through the flower entrance. When arriving bees entered and began to feed, they were overcome by the CO during the minute or so that is usually required to fill the crop, whereupon they rolled off the inclined feeding device into a large plastic funnel. The order of the bees from the bottom of the funnel tube reflected the order of arrival.

Care had to be taken to exclude ants. Although diffusion kept the CO concentration in the flower too low to anaesthetize bees, entering ants fell asleep in the tube and blocked the way. Ants were excluded by placing each station on an upturned plastic pail (Fig. 25) whose rim and indented bottom were filled with water. At the end of each experiment the caged foragers were allowed to revive at the forager station. In short experiments these bees almost always survived and could be reused (as decoys) on subsequent days. (The bees did not fly for some time after they became active, presumably because they remained blinded by the deoxygenation [Baumann and Mauro 1973].)

At the end of experiments, the recruits in each station were counted. After the first pair of experiments a new, previously unused odor was utilized each day. Since recruits were never exposed to a "familiar" food odor on a subsequent day, they could be marked and released at the hive entrance without the possibility of confusing the data in later experiments. Recruits which are anaesthetized soon after landing at a site forget the location anyway (Menzel, et al. 1974).

The feeding devices were washed each day. The stations were rinsed daily and dried in the sun.

The Locale

All of the experiments were performed in a relatively flat L-shaped field at The Rockefeller University Center for Field Research in Ecology and Ethology near Millbrook, New York. The field (Figs. 29 and 30) was bounded by trees on the west, south, and east. To the north and northeast the ground fell away rapidly into a valley. The hive was located in a small shed in the southwest corner of the field. The field was mowed and the cuttings removed between June 22-24, 1974 -- just before the experiments began.

The Weather

Wind direction and speed were measured by a calibrated Taylor Windscope (Lafayette # 13 F 74511W) and the values recorded every 2 seconds by Rustrak recorders. Temperature and humidity were recorded by the two-channel digital thermometer mentioned previously. Barometric pressure and sky conditions were recorded manually at 10-15 minute intervals.

Time of Day

Experiments 1 and 2 were performed at the end of the week of rain and cold weather which followed the mowing of the field. The hive was starving, and so responded very well to training. On subsequent days, however, natural sources provided serious competition. By beginning the experiments early in the day while the heavy dew was still on the vegetation, however, it was possible to obtain good results for about 2 hours.

DIRECTION COMMUNICATION AND ACCURACY

In order to test whether the dance communicates direction information -- and if so, with what accuracy -- Recruit Stations were set out in curved arrays. The artificial sun was used to "aim" the dances at particular stations. These experiments were all performed in the summer of 1974.

150 m Arrays

In experiments 2 and 4, the Forager Station was established 150 m north of the hive (Fig. 31), while Recruit Stations were set out at 22.5°,



Fig. 29. The Experimental Field. This view shows the southern end of the field. In the right background is the shed in which the hive was located. In the foreground are two recruit stations in part of a 150 m direction array.

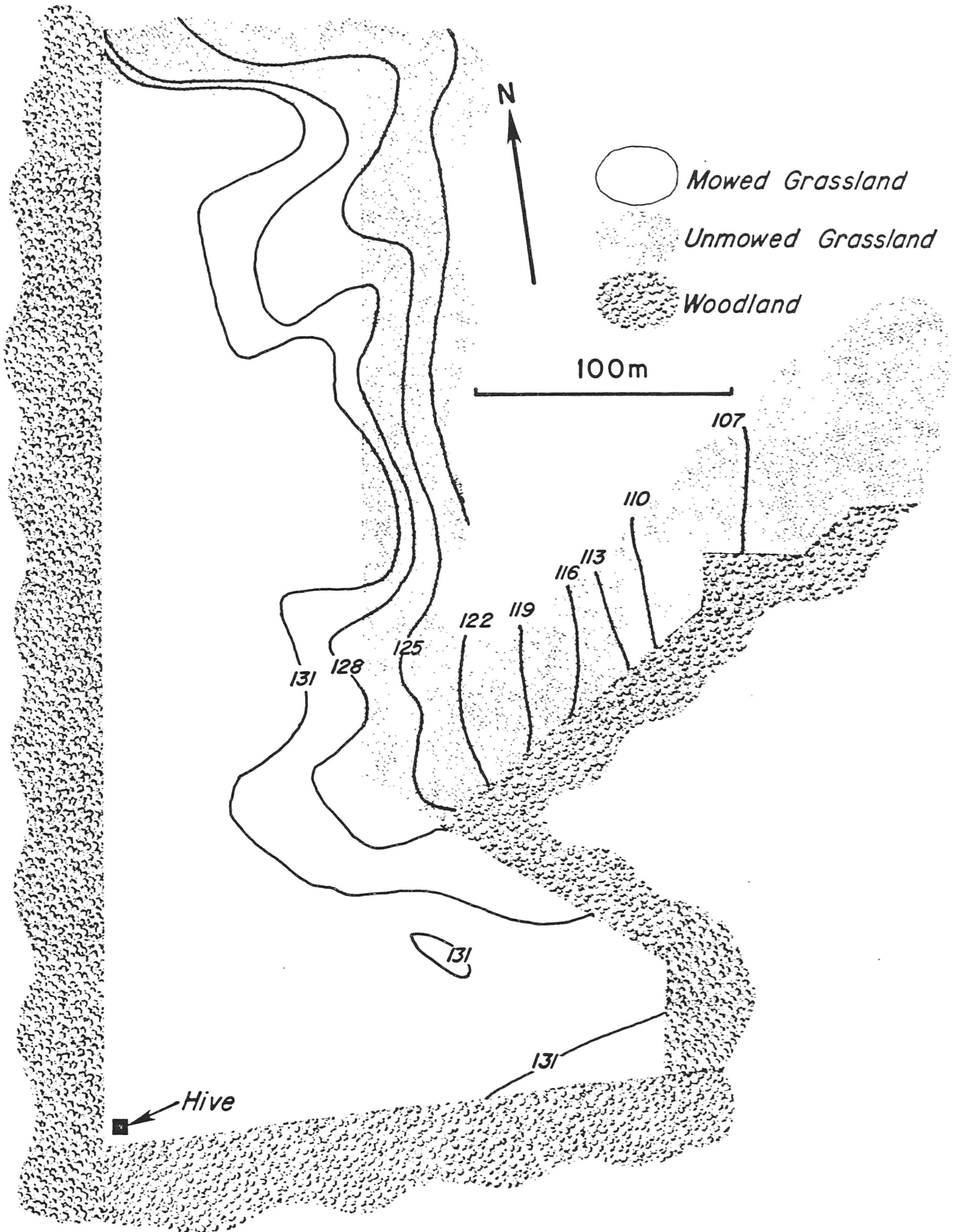


Fig. 30. Topographic Map of the Field. The field is bounded by woods on several sides. The shed with the hive is located in the southeast corner. Elevations are in meters above sea level.

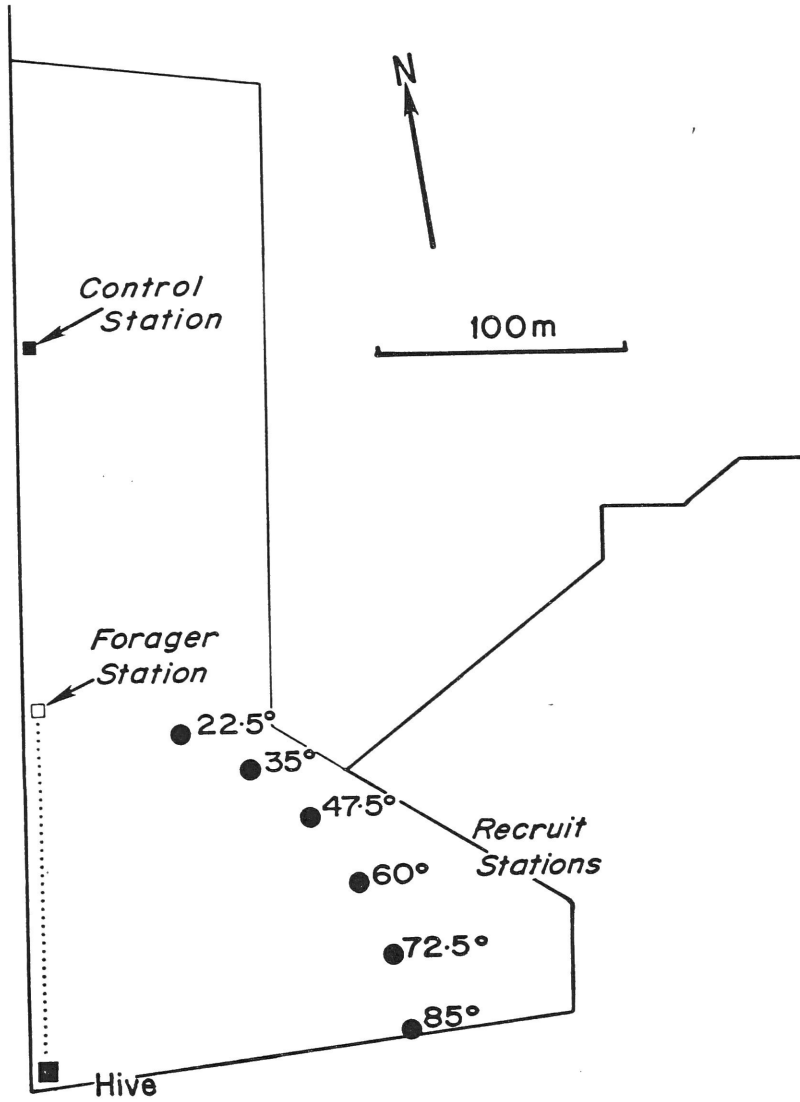


Fig. 31

Fig. 31. 150 m Direction Array. Foragers were trained to the Forager Station on a dilute orange-scented sucrose solution. During training their ocelli were covered with paint. A second group of foragers was trained to the Control Station on the same solution. Six Recruit Stations were set out 150 m from the hive in a $12\frac{1}{2}^\circ$ array as shown. These stations offered concentrated sucrose solutions containing the experimental scent. They were filled with CO to prevent entering recruits from returning to the hive. A cage of anaesthetized, ocelli-painted foragers was placed in each station to provide the appropriate bee and hive odors. When the experiment began, the solutions at the Forager and Control Stations were switched to concentrated experimental-scented and semi-concentrated anise-scented sucrose solutions, respectively. The light shining on the hive was moved from the "up" position to various angles left of vertical. The recruits (Figs. 32 and 33) arrived at Recruit Station at corresponding angles to the right of the Forager Station. For other details, see the text and Tables IV and V.

35°, 47.5°, 60°, 72.5°, and 85° to the right, 150 m from the hive. The Control Station was placed 300 m from the hive to the north. For experiment 2, the light shining on the dance area was placed at 85° to the left of vertical for 30 minutes. If dance direction is communicated, recruits would be expected to interpret these dances as indicating the station to the right of the Forager Station. In fact recruits did favor the 85° station (Fig. 32). The light was then moved to 35° left for 30 minutes, then changed to 60° left for another 30 minutes. Again, recruits favored the station indicated. On the average nine times as many recruits arrived at the station indicated by the dance as arrived at the other stations (Fig. 32). Had the bees been relying solely on olfactory cues, no preference for the station indicated by the dance could have been expected. The weather and data are summarized in Table IV.

In experiment 4, the procedure was repeated with similar results when the light direction was first 72.5° for 30 minutes, then 35° for the same period (Fig. 33). The data and weather are summarized in Table V. Again, recruits favored the station indicated by the dance. Since recruits went to the station specified by the dances of bees foraging in a completely different location, these experiments confirm unambiguously that recruit honey bees can use direction information contained in the dance in preference (or in addition) to site-specific odor information.

400 m Arrays

In order to test the accuracy of recruits more rigorously, the array was moved to 400 m and the angular interval reduced to 3° (Fig. 34). The size of the field made it necessary to establish the Forager and Control Stations to the northeast at 400 m and 500 m, respectively. The Recruit Stations were placed at 30°, 33°, 36°, 39°, 42°, and 45° to the left of the Forager Station. In experiment 7, the light shining on the dance floor was placed 42° to the right of vertical for 40 minutes, then moved to 33° for the same period. As in the previous experiments, the recruits showed a decided, though less dramatic preference for the indicated direction (Fig. 35). The data and weather are summarized in Table VI.

When this experiment was repeated, similar results were obtained (Fig. 36). In this case, the light was first 33° to the right of vertical for 40 minutes, then 42° right for the same period. The data and weather are summarized in Table VII.

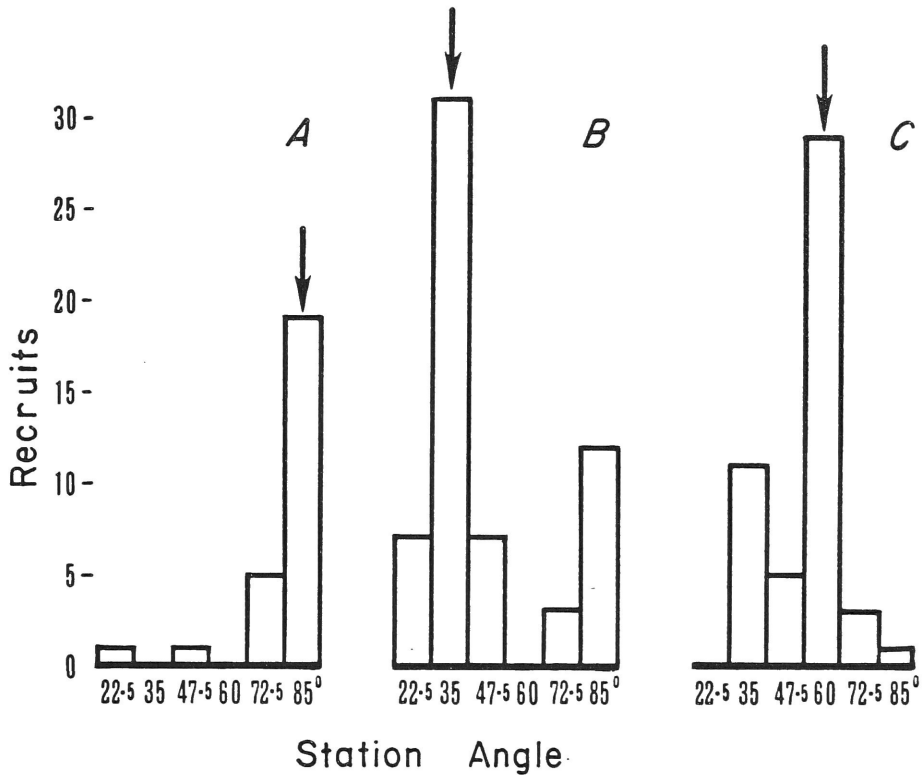


Fig. 32. Recruit Distribution in Experiment 2 (150 m Direction Array). The angle of the light shining on the hive is indicated by the arrows. A: for the first 30 minutes it was 85° left of vertical. During this period arrivals favored the Recruit Station 85° to the right of the Forager Station. B: during the second 30 minutes the light was at 35° left, and the recruits arrived predominantly in that direction. C: during the final 30 minutes, the light was 60° to the left, and the recruits favored that direction. For additional details see the text and Table IV.

Table IV

Time (EDT)		10:00	10:15	10:30	10:45	11:00	11:15	Totals
Dance Direction		83°	85°	36°	36°	58°	61°	
Recruits at Recruit Stations	22 1/2°	0	1	4	3	0	0	8
	35°	0	0	13	18	10	1	42
	47 1/2°	0	1	1	6	5	1	14
	60°	0	0	0	0	11	17	28
	72 1/2°	1	4	2	1	1	2	11
	85°	9	10	12	0	0	1	32 /135
Observed Dances		28	42	51	48	40	43	252
Forager Station:								
Forager Visits		41	51	54	44	45	45	280
Recruits		2	2	4	3	2	1	14
Weather:								Averages
Wind Direction		351°	005°	011°	007°	352°	356°	001°
Wind Speed (mph)		4.2	4.3	4.1	4.2	4.3	4.2	4.2
Sky Condition		Cdy	Cdy	Cdy	Cdy	Cdy	Cdy	Cdy
Pressure (mmHg)		771.6	771.6	771.6	771.6	771.6	771.6	771.6
Rel. Humidity (%)		62	63	63	64	64	64	63
Temperature (°C)		20	21	21	21	21	21	21

Table IV. Results of Experiment 2 (150 m Direction Array). The experiment was performed on June 28, 1974. The experimental scent was peppermint. The recruit distribution is shown in Fig. 32.

"Dance Direction" indicates the difference between the average direction of control forager dances and those of ocelli-treated foragers.

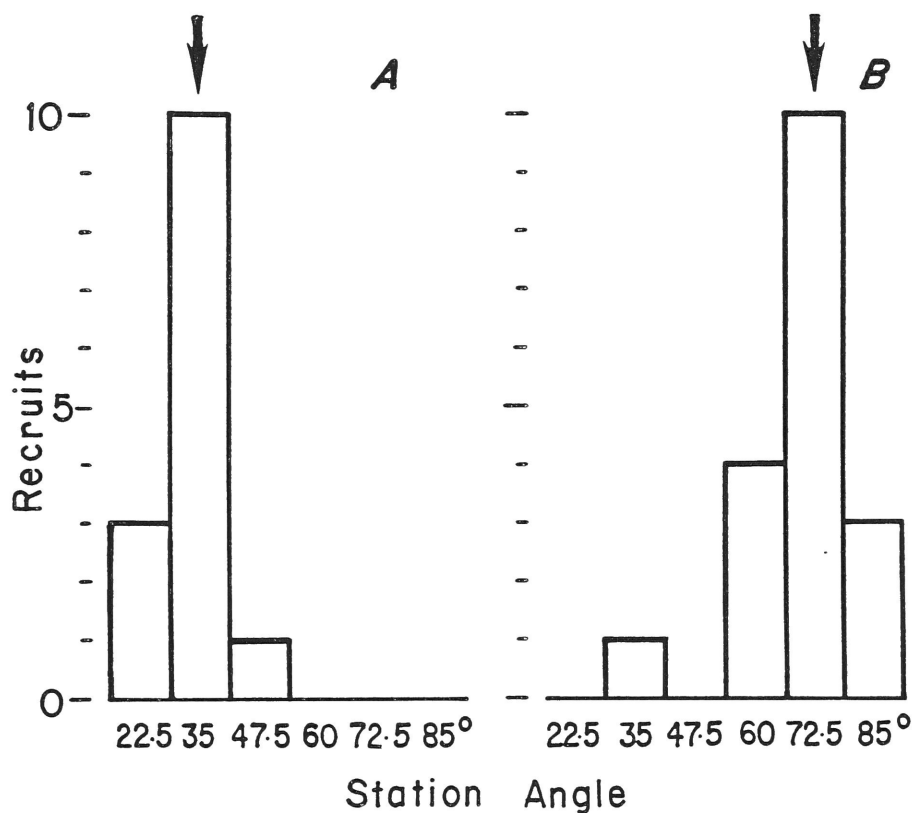


Fig. 33. Recruit Distribution in Experiment 4 (150 m Direction Array). The angle of the light shining on the hive is indicated by the arrows. A: for the first 30 minutes the light was placed 35° left of vertical. During this period the arrivals favored the Recruit Station located 35° to the right of the Forager Station. B: during the second 30 minutes the light was at 72 1/2° left, and the recruits arrived predominantly 72 1/2° to the right. For additional details, see the text and Table V.

Table V

Time (EDT)		9:20	9:30	9:40	9:50	10:00	10:10	Totals
Dance Direction		72°	75°	73°	34°	34°	35°	
Recruits at Recruit Stations	22 1/2°	0	0	0	0	2	1	3
	35°	0	0	0	3	2	5	10
	47 1/2°	0	0	0	1	2	1	4
	60°	0	1	0	0	0	0	1
	72 1/2°	1	6	3	1	0	0	11
	85°	1	1	1	0	0	0	3/ 32
Observed Dances		8	13	16	14	19	16	86
Forager Station:								
Forager Visits		19	19	22	18	21	18	117
Recruits		0	2	1	1	3	4	11
Weather:								Averages
Wind Direction		032°	029°	029°	032°	040°	032°	032°
Wind Speed (mph)		2.6	2.9	3.2	2.3	2.6	4.1	2.9
Sky Condition		Clr	Clr	Clr	Clr	Clr	Clr	Clr
Pressure (mmHg)		770.7	770.7	770.8	770.8	770.8	770.9	770.8
Rel. Humidity (%)		72	69	65	65	61	61	66
Temperature (°C)		21	22	22	22	23	23	22

Table V. Results of Experiment 4 (150 m Direction Array). The experiment was performed on July 16, 1974. The experimental scent was geranium bourbon. The recruit distribution is shown in Fig. 33.

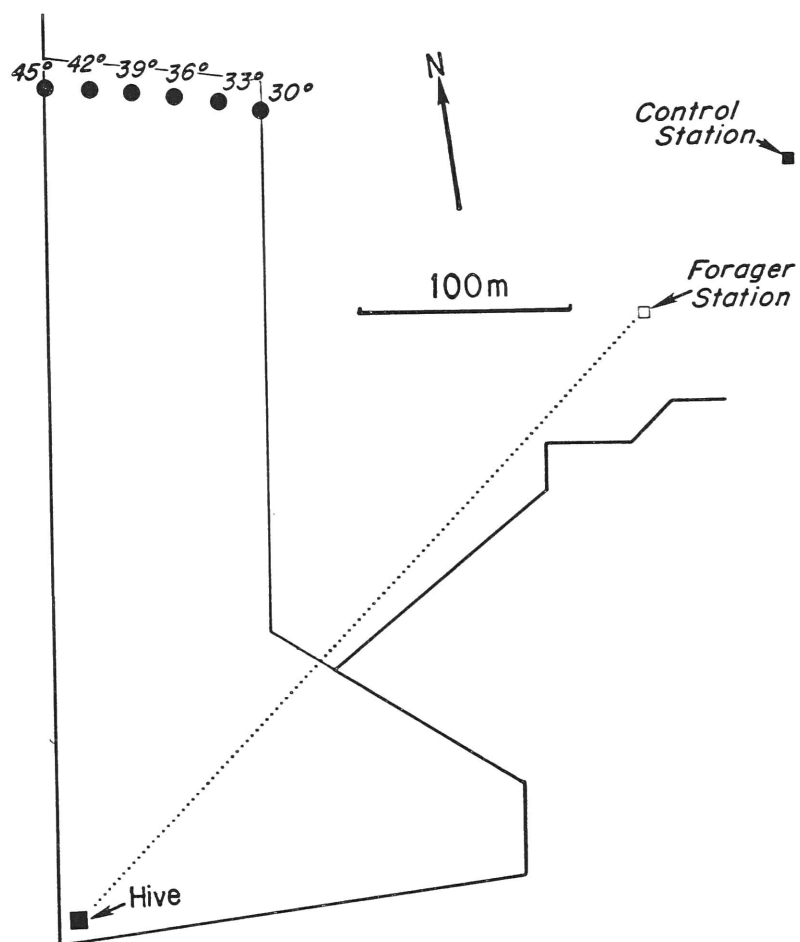


Fig. 34

Fig. 34. 400 m Direction Array. Ocelli-painted foragers were trained to the Forager Station 400 m from the hive. Control foragers were trained to the Control Station 500 m from the hive. Recruit Stations were set out 400 m from the hive at 3° intervals as shown. The light shining on the hive was used to misdirect recruits to the array of Recruit Stations. Recruits favored the indicated direction despite the greater distance and smaller angular separation of the stations (Figs. 35 and 36). For particulars, see the text and Tables VI and VII.

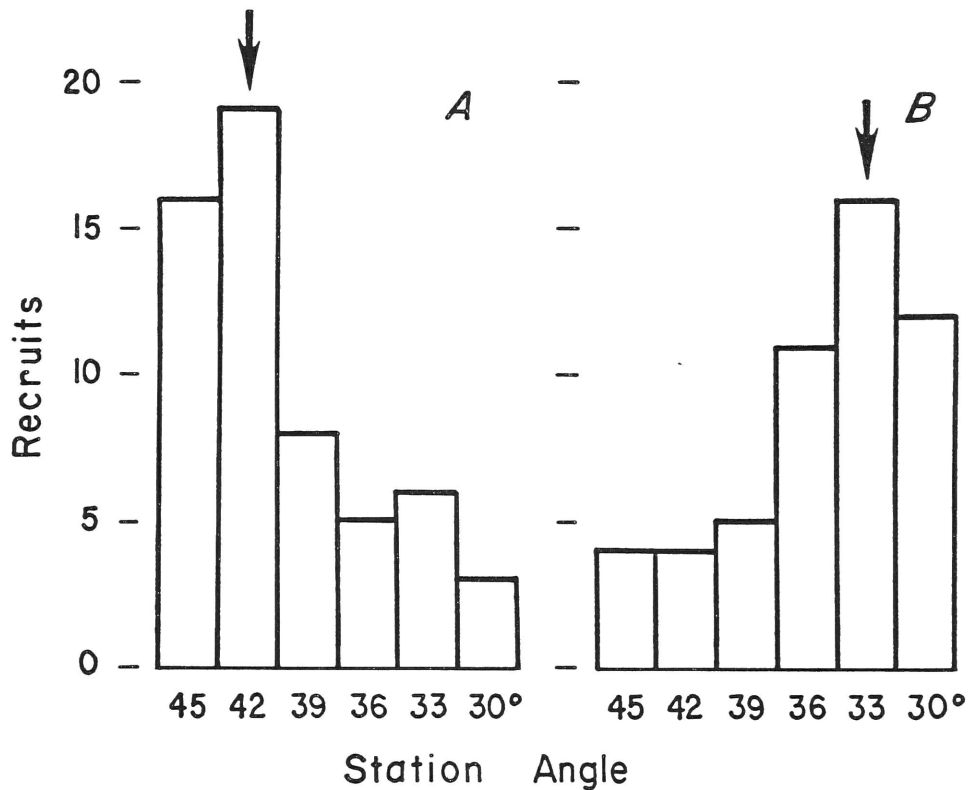


Fig. 35. Recruit Distribution in Experiment 7 (400 m Direction Array). The angle of the light shining on the hive is indicated by the arrows. A: for the first 40 minutes the light was placed 42° right of vertical. During this period the arrivals favored the Recruit Stations approximately 42° left of the Forager Station. B: during the last 40 minutes the light was placed at 33° right of vertical, and the recruits favored the stations approximately 33° left of the Forager Station. For additional details, see text and Table VI.

Table VI

Time (EDT)		9:00	9:20	9:40	10:00	Totals
Dance Direction		<u>42°</u>	<u>43°</u>	<u>34°</u>	<u>32°</u>	
Recruits at Recruit Stations	30°	1	2	6	6	15
	33°	3	3	6	10	22
	36°	2	3	5	6	16
	39°	3	5	4	1	13
	42°	9	10	0	4	23
	45°	6	10	3	1	20/ 109
Observed Dances		32	37	36	30	135
Forager Station:						
Forager Visits		41	48	40	43	172
Recruits		4	8	5	4	21
Weather:						Averages
Wind Direction		176°	167°	167°	172°	171°
Wind Speed (mph)		2.5	3.4	3.3	2.5	2.9
Sky Condition		Clr	Clr	Clr	Clr	Clr
Pressure (mmHg)		765.2	765.2	765.3	765.3	765.3
Rel. Humidity (%)		77	72	68	66	71
Temperature (°C)		26	27	28	28	28

Table VI. Results of Experiment 7 (400 m Direction Array). The experiment was performed on July 31, 1974. The experimental scent was rose absolute. The recruit distribution is shown in Fig. 35.

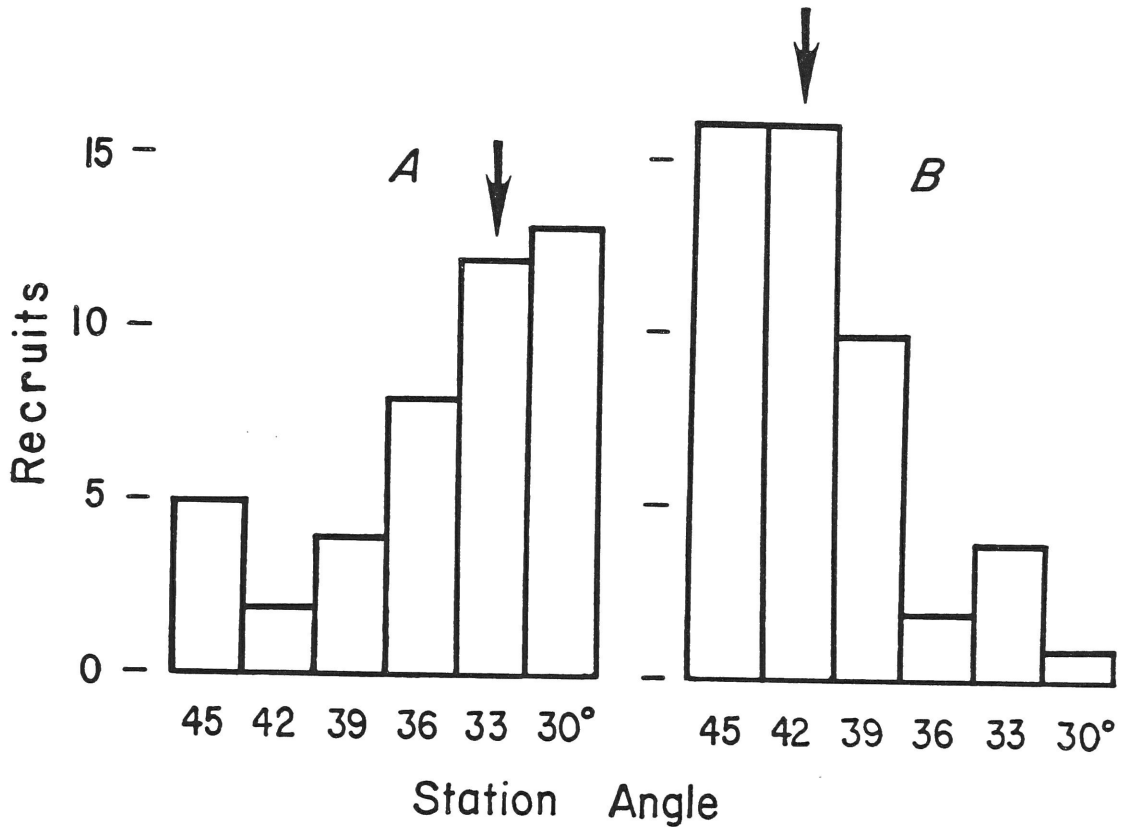


Fig. 36. Recruit Distribution in Experiment 8 (400 m Direction Array). The angle of the light is indicated by the arrows. A: for the first 40 minutes the light was placed 33° right of vertical. During this period the recruits favored the Recruit Stations approximately 33° left of the Forager Station. B: during the second 40 minutes the light was 42° right of vertical, and the recruits favored the Recruit Stations approximately 42° left of the Forager Station. For additional details see text and Table VII.

Table VII

Time (EDT)		9:00	9:20	9:40	10:00	Totals
Dance Direction		<u>33°</u>	<u>31°</u>	<u>43°</u>	<u>43°</u>	
Recruits at Recruit Stations	30°	8	5	1	0	14
	33°	6	6	2	2	16
	36°	3	5	1	1	10
	39°	3	1	5	5	14
	42°	1	1	5	11	18
	45°	3	2	8	8	21/ 94
Observed Dances		33	43	39	48	163
Forager Station:						
Forager Visits		49	55	55	56	215
Recruits		1	4	1	0	6
Weather:						Averages
Wind Direction		164°	149°	180°	174°	167°
Wind Speed (mph)		2.3	2.5	2.0	2.4	2.3
Sky Condition		Clr	Clr	Clr	Clr	Clr
Pressure (mmHg)		766.4	766.5	766.5	766.5	766.5
Rel. Humidity (%)		70	67	67	65	67
Temperature (°C)		24	25	26	27	25

Table VII. Results of Experiment 8 (400 m Direction Array). The experiment was performed on August 1, 1974. The experimental scent was rosemary. The recruit distribution is shown in Fig. 36.

Accuracy

As with von Frisch's fan experiments (Fig. 7), recruit accuracy in these experiments depended on the angular interval and/or distance (Fig. 37). Several factors limit the resolution of these measurements. Parallax error is introduced since the light is a finite distance away from the dance floor. From the dance attender's point of view, the angle of the light with respect to vertical varies with the location of the dance on the comb. Since the dancing was clustered (Fig. 27), the error was minimized. Figure 28 shows the distribution of parallax error calculated from Figure 27.

"Residual misdirection" must also be considered. The "error" in the transposition of the angle from light to gravity in the dance is apparently due to the earth's magnetic field (at least it disappears when the earth's field is cancelled; see Lindauer and Martin 1968). The magnitude of this error varies with dance direction (von Frisch 1967a, p. 216; see Fig. 38). No misdirection of recruits is thought to occur under ordinary conditions (von Frisch 1967a, pp. 212-213), since both dancers and dance attenders make the same transposition errors. This would be true, however, only if the orientation of dance attenders with respect to gravity exactly paralleled that of the dancers. In reality, attenders orient toward the dancer, usually at about a 40° angle to the left or right of the straight run. Attenders which successfully maintain antennal contact for several cycles generally follow the waggle runs from alternate sides. Closer analysis reveals their strategy for maintaining contact (Fig. 38). This alternation creates a distinctly different residual misdirection curve for attenders (Fig. 39).

With the artificial sun, however, the problem is entirely different. The orientation of untreated recruits to the light is free of residual misdirection effects, while that of the ocelli-painted foragers is not. In order to compensate for residual misdirection in the 3° array experiments, the angle of the light was adjusted slightly at the beginning of the experiment until the average orientation of the treated foragers' dances was correct. This corresponded to a dance direction of about 280° . As the experiment continued, further corrections were made each 30 minutes on the

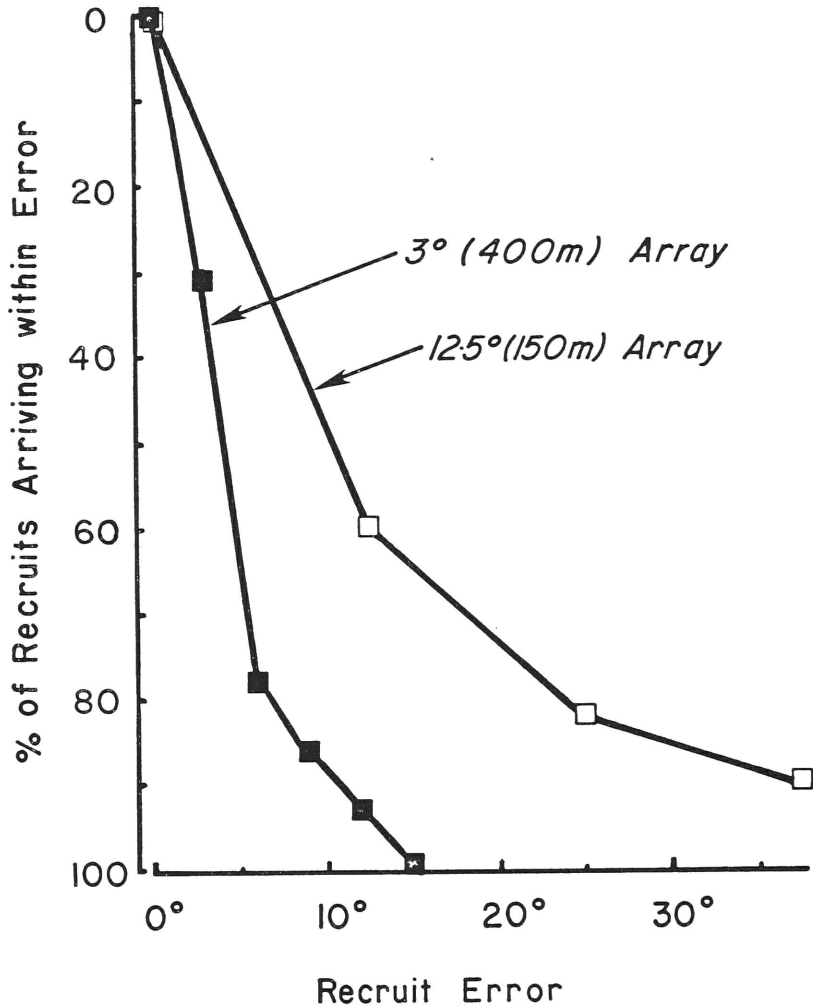


Fig. 37. Recruit Direction Accuracy. Recruit accuracy for the 150 m and 400 m direction arrays is plotted. "Recruit error" is taken as the distance from the "target" specified by the dancing. These values may be compared (with caution) to those from von Frisch's fan experiments (Fig. 6). As will be demonstrated later, von Frisch's techniques increase the apparent accuracy of recruits. It should also be noted that this data is from a one-dimensional array of stations, whereas searching honey bee recruits are distributed in two dimensions. As will be discussed later, the actual accuracy of recruits may be less than this figure indicates.

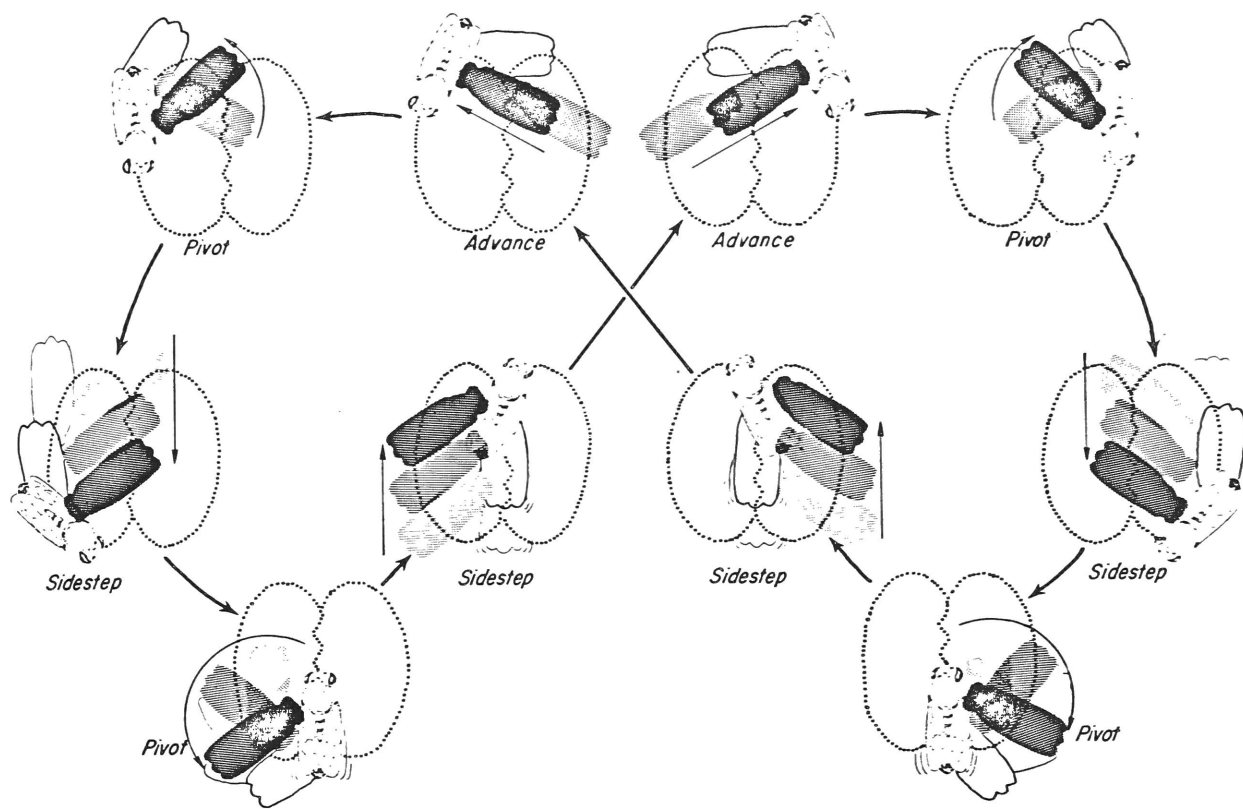


Fig. 38. Dance Following Strategy. Dance attenders which regularly maintain contact with several cycles of a dance seem to utilize a single, regular strategy. These attenders follow the dance from the side away from which the dancer will turn on its next return run. The attender sidesteps during the waggle run, maintaining approximately the same orientation with respect to gravity. When the dancer turns away at the beginning of the return, the attender advances, thereby cutting off attenders which have been "watching" from the other side. As the dancer continues its return, the attender must pivot, sidestep again, and then pivot again as the dancer turns again into the waggle run. At this point the attender is again on the side away from which the dancer will turn. Whether this strategy correlates with greater recruit success is another question. This strategy fails when, as happens rarely, the dancer turns to the same side two runs in a row. The drawing is based on single-frame analysis of dances filmed at 64 fps. Quantitative data on this phenomenon are being gathered for a more detailed analysis.

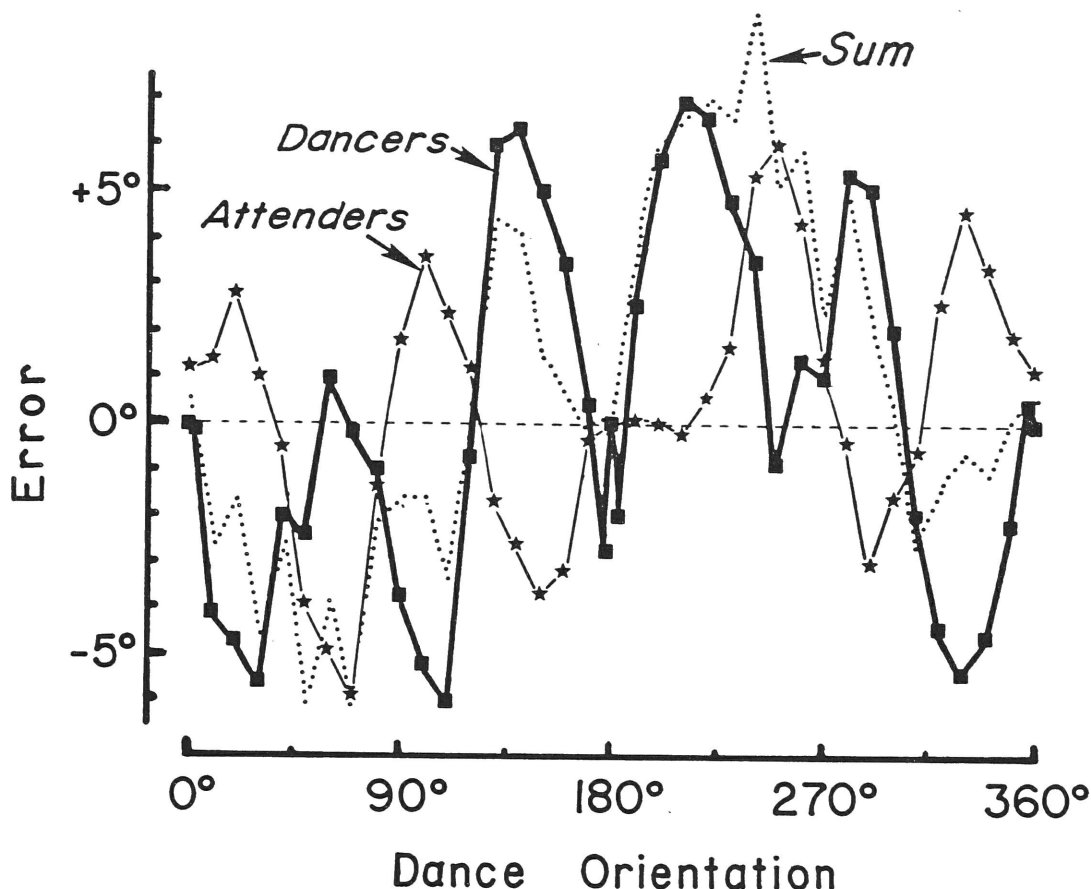


Fig. 39. Residual Misdirection. Dancing foragers make errors in transposing the angle to the station with respect to the sun, to an angle with respect to gravity. Data from von Frisch (1967a, p. 216) is plotted here ("Dancer" curve), although there is variance in the error. Assuming the sense organs of the attenders are similar, their misdirection after attending an equal number of waggle runs from each side can also be approximately calculated by assuming an average orientation with respect to the dancer. (For example, if the attenders followed the waggle runs at a 40° angle to the right and left, then recruit misdirection would be the average of dances 40° to the right and left of the dance being attended.) The sum of Forager-dance and recruit-following misdirections should represent the net misdirection of searching recruits. On the average, this error is a small but inherent constraint on the overall accuracy of direction communication.

basis of Figure 39 and earlier measurements. Since the amount of misdirection depends on the dance orientation, which in turn depends on the position of the sun with respect to the food, which changes as the sun moves, this correction had to be itself periodically corrected. Analysis of the video tapes revealed that residual misdirection accounted for an average error of $\pm 0.8^\circ$ in the dance direction. The hive was shielded from the magnetic field to a great extent by the metal shed. The hive's orientation was north-south.

If "accuracy" is taken to mean the mean error -- that is, the angles within which half of the recruits are to be found -- then the accuracy of the recruits in the 3° (400 m) experiments was $\pm 4.2^\circ$ (Fig. 41); of course, the finite size of the array necessarily results in some recruits being "off the edge." To minimize this problem in the data, the results from the end station next to the "target" can be excluded. This procedure yields an accuracy of $\pm 3.9^\circ$. The mean accuracy in the 12.5° (150 m) experiments was $\pm 11.9^\circ$. The limit of the technique due to parallax and uncorrected misdirection was $\pm 1.4^\circ$.

These experiments are not strictly comparable with those of von Frisch (summarized in Fig. 7; his data indicate mean recruit accuracies of $\pm 5.8^\circ$ in the 8° array, and, in the 15° arrays, means of $\pm 10.6^\circ$ at 200 m, $\pm 5.7^\circ$ at 550 m). In his fan experiments (Fig. 6) the Forager Station was located in the middle of the array. Recruit stations offered no hive odor, no visual landing encouragement, and no scent gland odor. Recruits were not captured except at the Forager Station (and recruits of the Forager Station are not included in Fig. 7). Since the accuracy of recruits may vary with both the distance and the spacing of the stations, the arrays used here may also be expected to bias the observed accuracy.

Effects of the von Frisch Techniques

In order to examine more closely the effects of von Frisch's techniques, the 3° array was used with the Forager Station in the middle or at the end. The stations were modified so that entering recruits could not feed. After passing through the photo-electric counter, the bees could only walk up and out of the station. Hence, the same bee could be counted more than once. The stations had neither CO nor anaesthetized foragers. Recruits arriving at the Forager Station were captured.

In the first experiment, the Forager Station was placed 20 m behind a middle Recruit Station (Fig. 40). The light was in the "up" position in the hive, thereby producing no misdirection. The experiment lasted 50 minutes. As expected, recruits favored the stations in the direction of the Forager Station (Fig. 41A; see Table VIII). The mean accuracy was $\pm 3.3^\circ$ (excluding recruits at the Forager Station), indicating that under these conditions, von Frisch's techniques may increase the apparent accuracy of recruits.

To test whether von Frisch's techniques might be having any other effects on recruit distribution, the experiment was repeated with the Forager Station behind an end Recruit Station (Fig. 42). The light in the hive was placed 15° to the right of vertical so that the dancing would misdirect the recruits to the 15° station at the other end of the array. If von Frisch's techniques have any effect on recruit distribution, an enhancement of recruit arrivals at the east end of the array would be expected.

The experiment lasted for 50 minutes. Although the west end (indicated by the dancing) did receive twice as many recruits as the stations in the middle of the array, the stations at the east (forager) end received nearly 5 times more (Fig. 41B; see Table IX). Under these conditions, then, having the Forager Station near the array can affect recruit distribution. Without misdirection, however, these effects are masked.

Effects of Wenner's Techniques

A major difference between my experiments and Wenner's lies in his training technique (Wenner 1961). In order to examine the effect of this difference, a 150 m (12.5°) array direction experiment (Fig. 31) was performed after training the foragers in his way (on 2 M sucrose containing the experimental scent). In the first experiment, the light was moved to 85° left of vertical for 30 minutes, then to 22.5° left for another 30 minutes. For the second experiment, the light was first at 22.5° for 30 minutes, then moved to 85° for the same period. The results of these two experiments are shown in Figures 43 and 44 (the data and weather are summarized in Tables X and XI). Just as Johnson (1967a) found, recruits

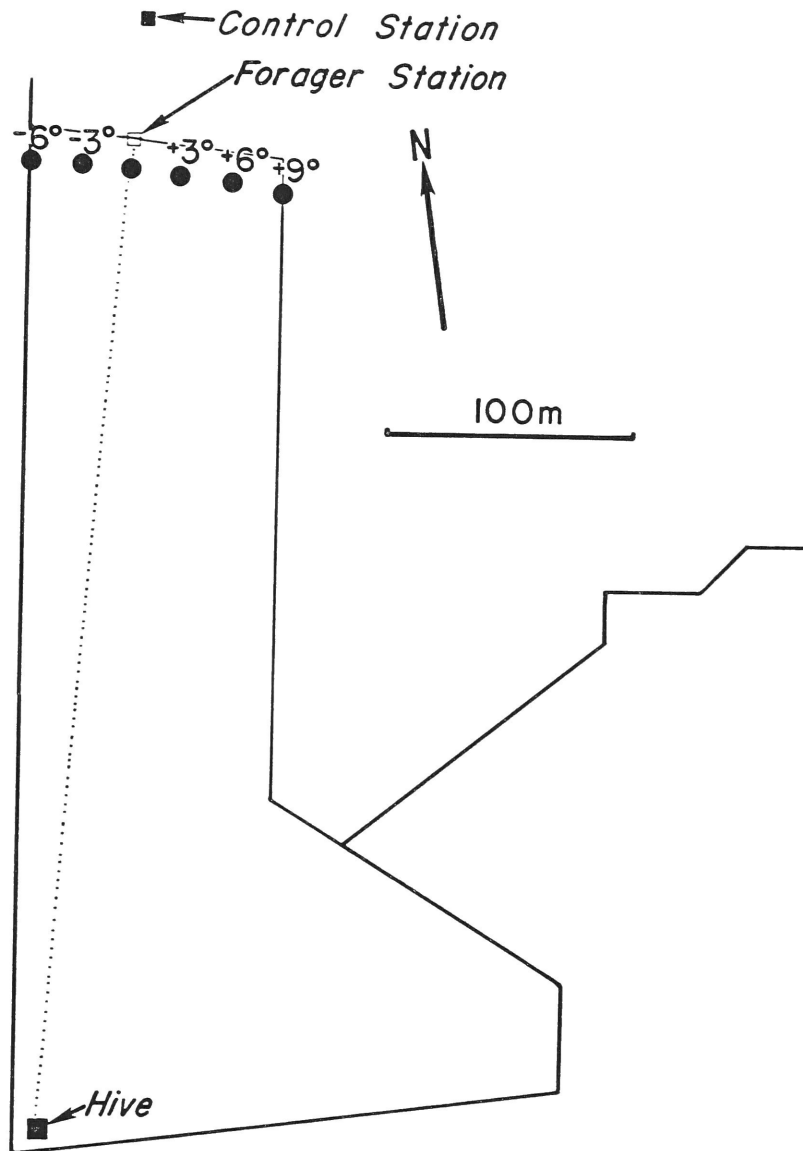


Fig. 40

Fig. 40. Von Frisch Direction Control Array I. Ocelli-painted foragers were trained to the Forager Station 410 m from the hive. Control foragers were trained to the Control Station 460 m from the hive. Recruit Stations were set out 390 m from the hive at 3° intervals as shown. (In von Frisch's experiments the stations were 8° or 15° apart and the Forager Station 50 m from the array.) Unlike previous (and subsequent) experiments, the Recruit Stations were modified so that entering recruits could not feed. The design also allowed the recruits to escape quickly, just as in von Frisch's fan experiments. These stations also lacked the anaesthetized foragers to provide hive and bee odors. The light was placed in the "up" position so that the dances signalled the actual direction of the Forager Station. The recruit distribution is shown in Fig. 41a.

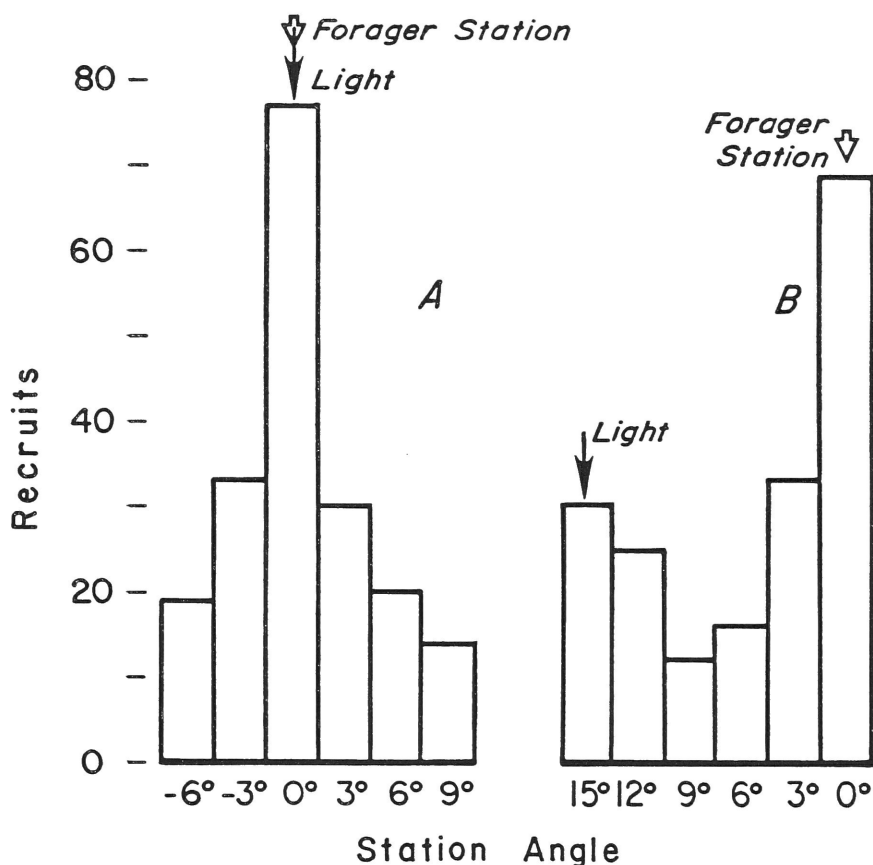


Fig. 41. Recruit Distribution in Experiments 9 and 10 (von Frisch Direction Controls). A: recruit distribution in experiment 9. When the light was in the "up" position, the forager dances indicated the actual direction of the Forager Station. Recruits favored the Recruit Station in the same direction. For additional details see text, Fig. 40, and Table VIII. B: recruit distribution in experiment 10. When the light was placed 15° to the right of vertical, the recruits nevertheless favored the Recruit Station near the Forager Station. A secondary preference for the dance direction is also apparent. Presumably the presence of the Forager Station so near the array of Recruit Stations affected the recruit distribution. For additional details, see text, Fig. 42, and Table IX.

Table VIII

Time (EDT)		9:00	9:10	9:20	9:30	9:40	9:50	Totals
Dance Direction		+2°	+1°	-1°	+1°	0°	+1°	
Recruits at Recruit Stations	+9°	2	1	3	4	2	2	14
	+6°	1	3	6	3	5	2	20
	+3°	2	5	4	5	8	6	30
	0°	9	10	12	14	14	18	77
	-3°	6	3	6	8	6	4	33
	-6°	2	5	1	5	4	2	19/ 193
Observed Dances		11	16	18	21	14	12	92
Forager Station:								
Forager Visits		20	26	29	25	29	21	150
Recruits		5	11	17	18	21	16	88
Weather:								Averages
Wind Direction		007°	026°	005°	039°	056°	055°	037°
Wind Speed (mph)		0	0.1	1.0	0.5	0	0.1	0.6
Sky Condition		Hzy	Hzy	Hzy	Hzy	Hzy	Hzy	Hzy
Pressure (mmHg)		768.3	768.3	768.3	768.3	768.3	768.3	768.3
Rel. Humidity (%)		78	71	68	68	68	65	69
Temperature (°C)		25	26	27	27	27	28	27

Table VIII. Results of Experiment 9 (von Frisch Control). The Experiment was performed on August 2, 1974. The experimental scent was sassafrass. The recruit distribution is shown in Fig. 41a.

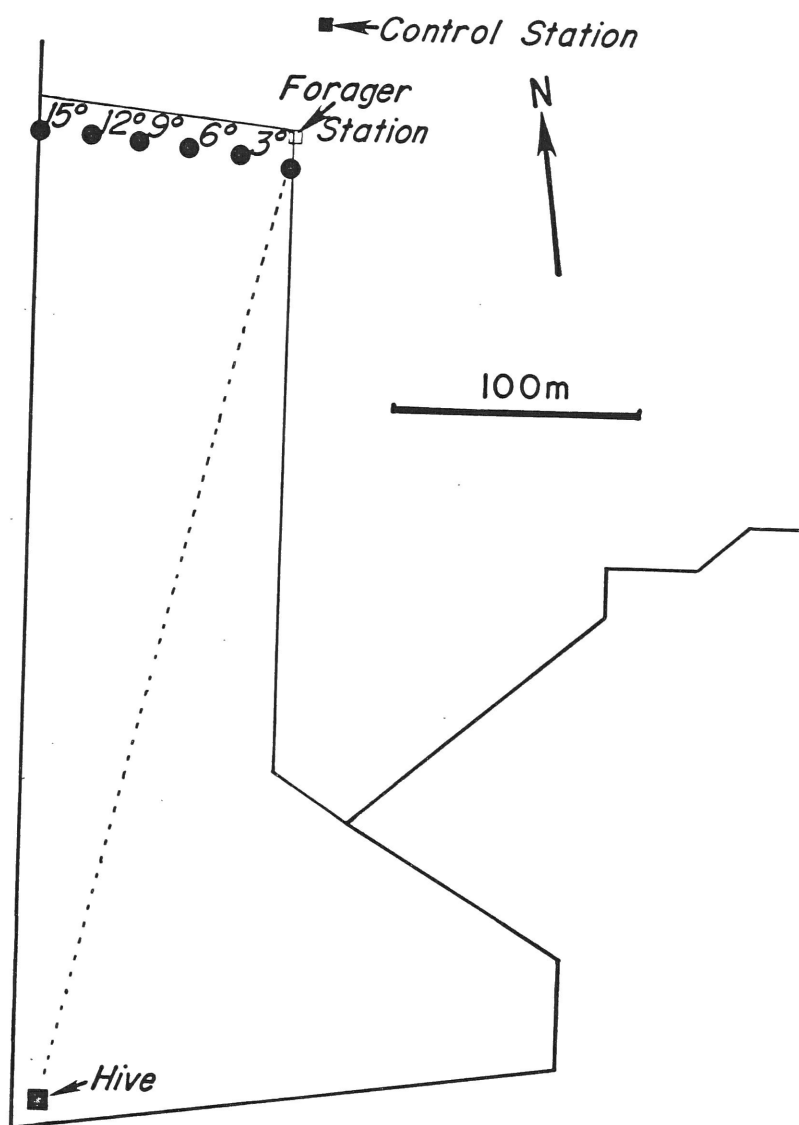


Fig. 42

Fig. 42. Von Frisch Direction Control Array II. Ocelli-painted foragers were trained to the Forager Station at 410 m. Control foragers were trained to the Control Station 460 m from the hive. Recruit Stations were set out at 3° intervals as shown. As in experiment 9, the Recruit Stations were modified to allow recruit escape, prevent feeding, and to eliminate bee and hive odors -- thereby approximating the conditions of von Frisch's fan experiments. The light was placed 15° to the right of vertical, thereby causing the dances to specify the station 15° to the left of the Forager Station. The recruit distribution is shown in Fig. 41b.

Table IX

Time (EDT)		9:00	9:10	9:20	9:30	9:40	Totals
Dance Direction		14°	15°	13°	15°	16°	
Recruits at Recruit Stations	0°	7	14	18	10	19	68
	3°	2	8	9	4	11	34
	6°	2	2	4	2	5	15
	9°	1	4	2	1	4	12
	12°	3	6	6	4	5	24
	15°	3	6	8	7	6	30/ 183
Observed Dances		8	15	18	22	19	82
Forager Station:							
Forager Visits		15	16	19	23	22	95
Recruits		8	18	21	14	19	80
Weather:							Averages
Wind Direction		004°	003°	006°	357°	020°	006°
Wind Speed (mph)		0	0	1.2	1.9	2.5	1.1
Sky Condition		PC	PC	PC	PC	PC	PC
Pressure (mmHg)		766.6	766.6	766.6	766.6	766.6	766.6
Rel. Humidity (%)		80	76	76	76	73	76
Temperature (°C)		28	29	29	29	29	29

Table IX. Results of Experiment 10 (von Frisch Control). The experiment was performed on August 4, 1974. The experimental scent was ylang ylang. The recruit distribution is shown in Fig. 41b.

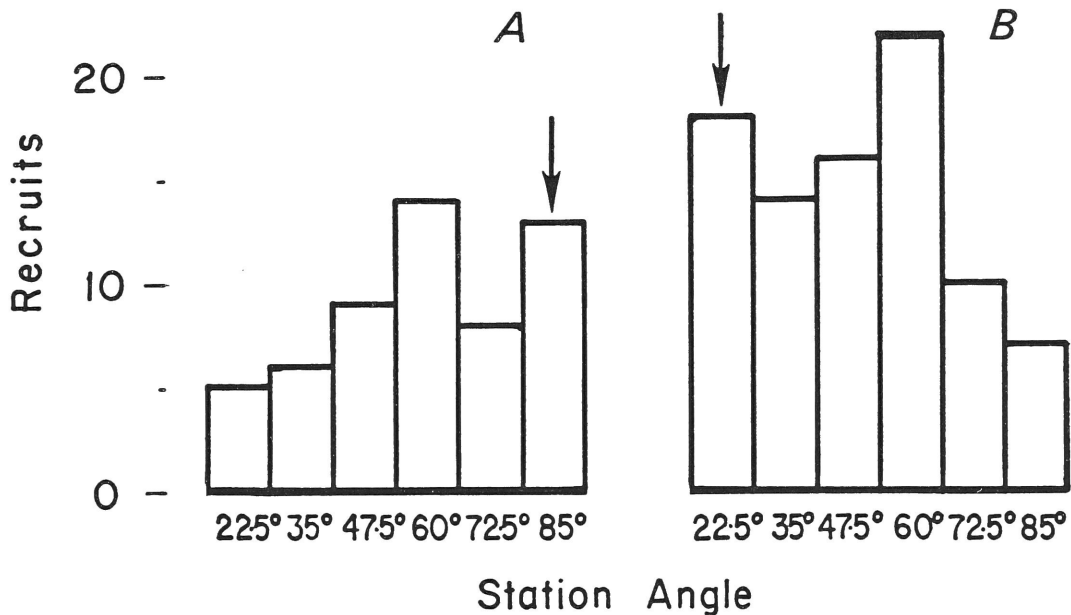


Fig. 43. Recruit Distribution in Experiment 15 (Wenner Direction Control). Foragers were trained according to Wenner's technique -- on a concentrated sucrose solution containing the experimental scent. A: during the first 30 minutes the light shining on the hive was placed 85° to the left of vertical. Recruits showed little or no preference for the dance direction (arrow). These results are in sharp contrast to those obtained using the normal training technique (see Figs. 32 and 33). For additional details, see text and Table X.

Table X

Time (EDT)		9:40	9:50	10:00	10:10	10:20	10:30	Totals
Dance Direction		87°	87°	85°	22°	24°	21°	
Recruits at Recruit Stations	22-1/2°	1	3	1	6	5	7	23
	35°	2	1	3	3	3	8	20
	47-1/2°	2	4	3	4	4	8	25
	60°	6	3	5	5	6	11	36
	72-1/2°	2	4	2	2	4	4	18
	85°	3	4	6	2	1	4	20/ 142
Observed Dances		12	9	8	11	15	10	65
Forager Station:								
Forager Visits		21	16	15	19	15	18	104
Recruits		6	6	7	9	5	8	41
Weather:								Averages
Wind Direction		188°	181°	195°	192°	193°	195°	191°
Wind Speed (mph)		1.1	1.0	0.9	0.9	0.7	0.5	0.9
Sky Condition		Clr	Clr	Clr	Clr	Clr	Clr	Clr
Pressure (mmHg)		752.7	752.7	752.7	752.7	752.7	752.7	752.7
Rel. Humidity (%)		64	64	64	60	57	57	61
Temperature (°C)		21	21	21	22	22	23	22

Table X. Results of Experiment 15 (Wenner Direction Control). The experiment was performed on August 10, 1974. The experimental scent was rose absolute. The recruit distribution is shown in Fig. 43.

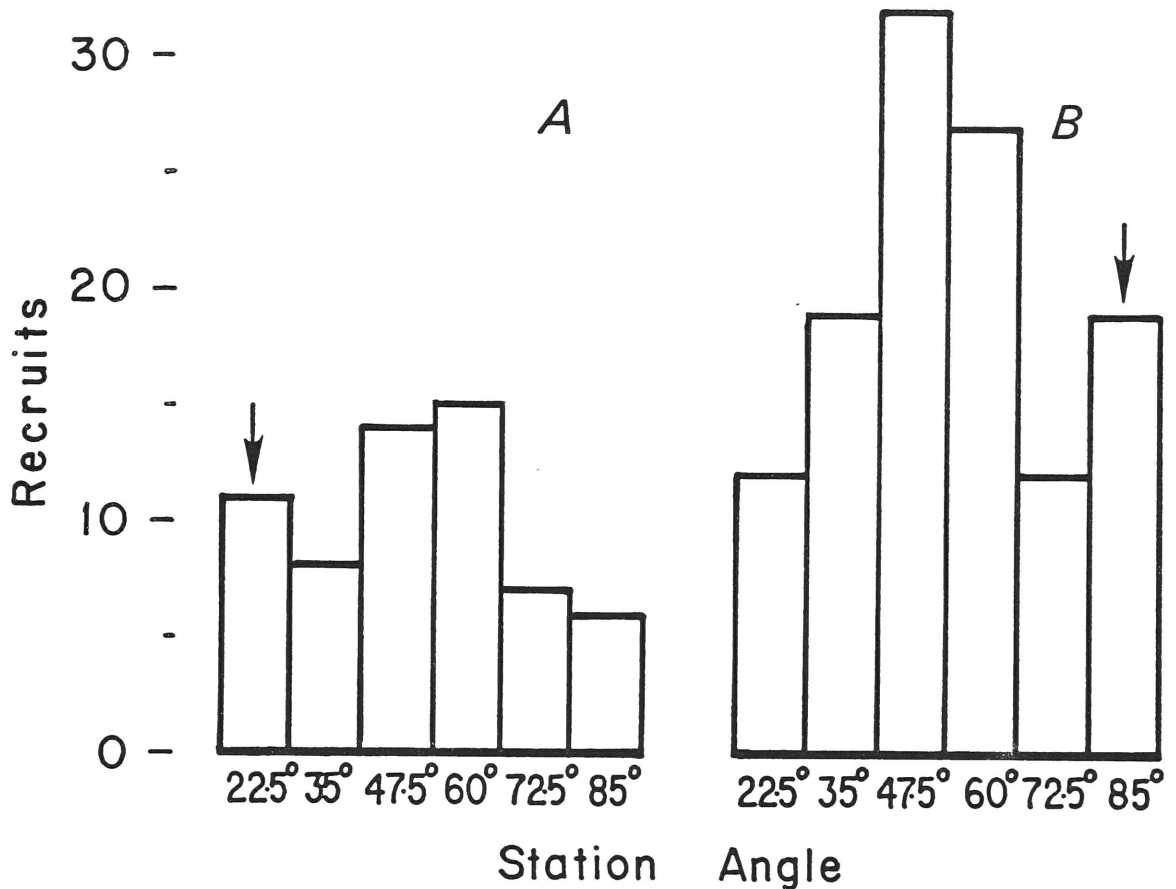


Fig. 44. Recruit Distribution in Experiment 16 (Wenner Direction Control). Foragers were trained according to Wenner's technique. A: during the first 30 minutes the light shining on the hive was placed at $22\frac{1}{2}^{\circ}$ left of vertical. Recruits showed little or no preference for the direction specified by the dancing (indicated by the arrow). B: during the second 30 minutes the light was placed 85° to the left of vertical. Again, recruits showed little or no preference for the direction indicated by the dancing (arrow). For additional details, see text and Table XI.

Table XI

Time (EDT)		9:00	9:10	9:20	9:30	9:40	9:50	Totals
Dance Direction		20°	22°	22°	83°	86°	86°	
Recruits at Recruit Stations	22-1/2°	2	6	3	4	3	5	22
	35°	4	0	4	4	8	6	26
	47-1/2°	3	6	5	8	7	17	46
	60°	3	3	9	4	11	12	42
	72-1/2°	2	2	3	3	2	7	19
	85°	3	1	2	9	2	7	24
Observed Dances		13	16	10	10	15	14	78
Forager Station:								
Forager Visits		23	21	16	19	15	18	112
Recruits		9	5	8	11	6	5	44
Weather:								Averages
Wind Direction		343°	005°	340°	004°	011°	007°	358°
Wind Speed (mph)		3.3	3.7	3.5	3.1	4.3	4.5	3.4
Sky Condition		Clr	Clr	Clr	Clr	Clr	Clr	Clr
Pressure (mmHg)		772.7	772.7	772.7	772.7	772.6	772.6	772.7
Rel. Humidity (%)		73	65	65	62	58	58	67
Temperature (°C)		22	23	23	24	24	24	23

Table XI. Results of Experiment 16 (Wenner Direction Control). The experiment was performed on August 11, 1974. The experimental scent was rosemary. The recruit distribution is shown in Fig. 44.

avored the center of the array even when the dancing specified stations at the edge. In these experiments the center station averaged 1.2 times as many recruits as the end station specified by the dancing, and 2.5 times as many as the other end station. Thus recruits, under these conditions, do not seem to use the direction information contained in the dance.

Under these conditions, the Wenner training technique appears to strongly affect the distribution of recruits. The exact mechanism of the effect is not known. The use of high concentrations of sucrose during training might recruit bees which are unable to locate the rapidly-moving Forager Station. These "lost" bees may later rely on odor alone. Alternatively, the use of high levels of experimental scent during training may simply cause recruitment to odor without dancing, as von Frisch (1967a, pp. 23, 30-35, 152-153, 257-264) had found earlier.

DISTANCE COMMUNICATION AND ACCURACY

Short-Distance Experiments

In order to determine whether distance information is communicated in the dance the Forager Station was placed 60 m to the north, and a line of Recruit Stations was set out at 30 m intervals to the east, 85° to the right of the Forager Station (Fig. 45). The light was placed 85° to the left of vertical in order to direct recruits to the array of Recruit Stations instead of to the Forager Station. If the dance does not communicate distance information, recruits should show no preference for the correct distance. The training solution was then replaced with the experimental solution, and the Forager Station moved to 90 m. After 30 minutes, the Forager Station was moved to 120 m, and so on at 30 m intervals to 150 m, 180 m, 210 m, 150 m, 90 m, and finally 60 m. The distribution of recruits to the east did accurately reflect the distance of the Forager Station (Fig. 46; these data are summarized in Table XII). The experiment was repeated in the order 210 m (20 min.), 180 m (10 min.), 150 m (20 min.), and 90 m (20 min.). Again, recruits showed a preference for the station in the array of Recruit Stations at the same distance as the former station. The recruits are shown in Figure 47 (see Table XIII). From these two experiments, it is clear that distance information is communicated to and used by recruited bees.

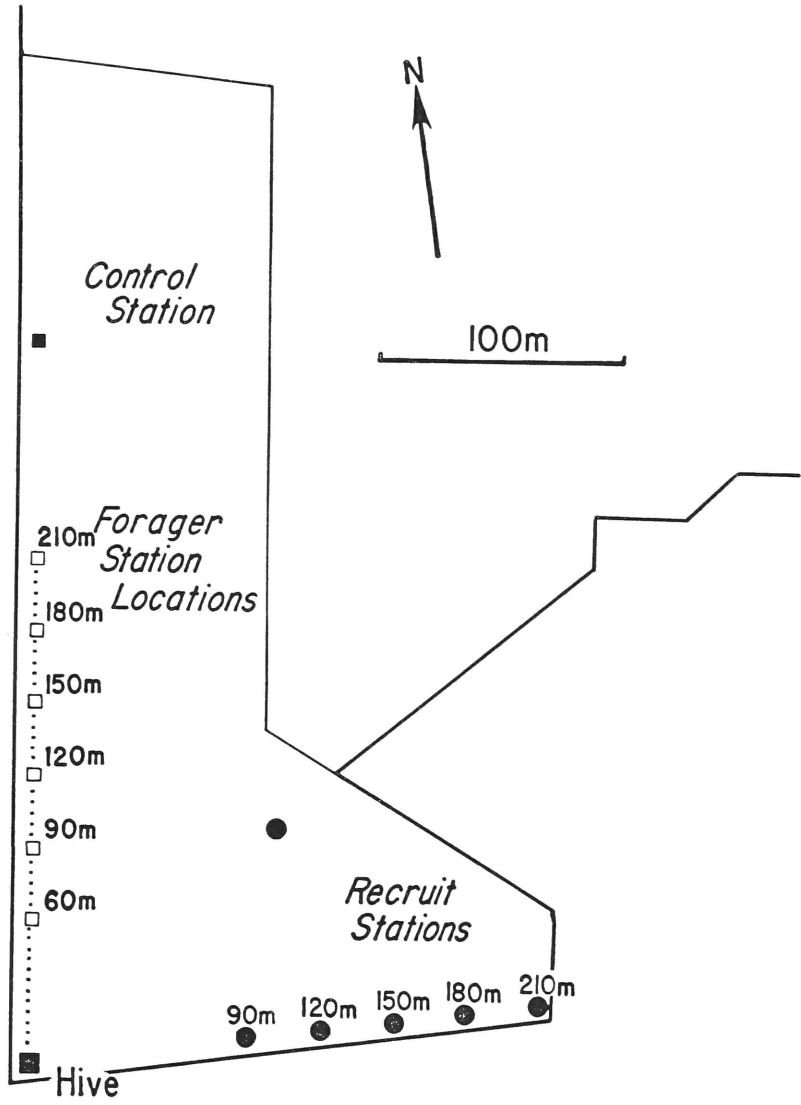


Fig. 45

Fig. 45. Closer Distance Array. Ocelli-painted foragers were trained to the north to the Forager Station. Control foragers were trained to the Control Station located 300 m from the hive. Recruit Stations were set out at 30 m intervals from 90-210 m on a line 85° to the right of the Forager Station. An "Intermediate" Recruit Station was placed $42\frac{1}{2}^\circ$ to the right of the Forager Station and 150 m from the hive. A light shining on the hive caused recruits to search for the food in the direction of the Recruit Station array. From time to time the Forager Station was moved to a different distance from the hive. Recruits favored the Recruit Station at the same distance as the Forager Station (Figs. 46 and 47). For particulars, see text and Tables XII and XIII.

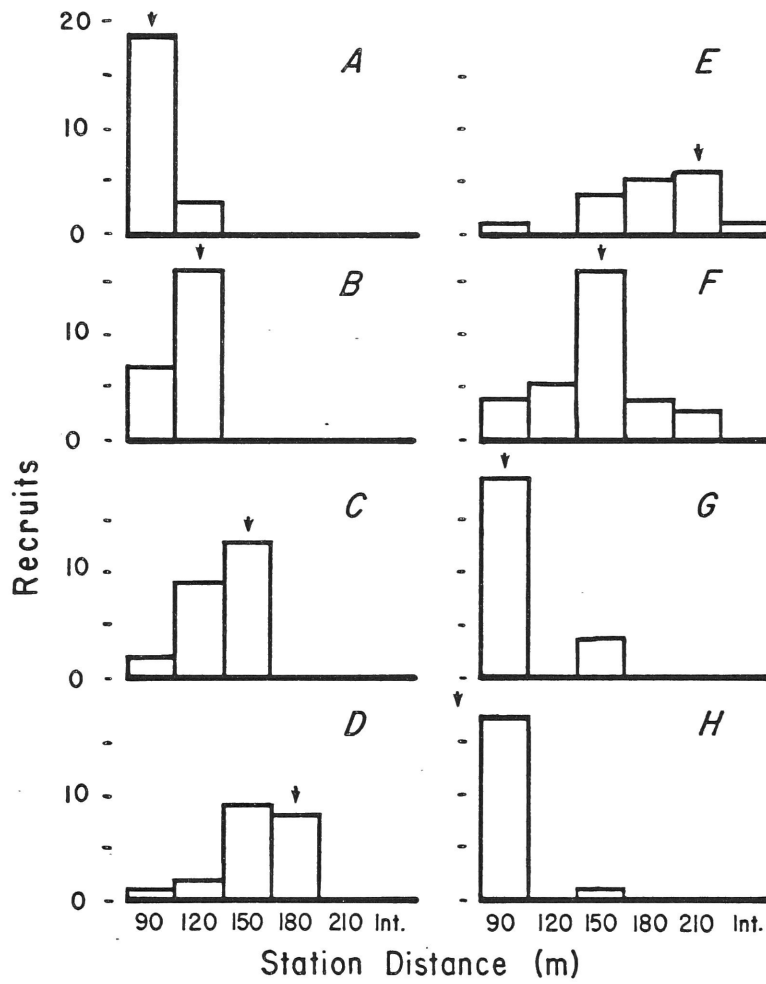


Fig. 46

Fig. 46. Recruit Distribution in Experiment 1 (Closer Distance Array).
The distance of the Forager Station is indicated by the
arrows (in "H" the Forager Station was at 60 m). The Forager
Station was moved at 20 minute intervals in the order shown.
Recruits favored the Recruit Station at the distance indicated
by the dances. For additional details, see text and Table XII.

Table XII

Time (EDT)	9:55	10:15	10:35	10:55	11:15	11:35	11:55	12:15	Totals
Dance Direction	84°	84°	85°	87°	85°	85°	82°	86°	
Distance	90m	120m	150m	180m	210m	150m	90m	60m	
Recruits at Recruit Stations	90m	120m	150m	180m	210m	150m	90m	60m	
	19	7	2	1	1	4	19	17	70
	3	16	9	2	0	5	0	0	35
	0	0	13	9	4	16	4	1	47
	0	0	0	8	5	4	0	0	17
	0	0	0	0	6	3	0	0	9
Int.	0	0	0	0	1	0	0	0	1/179
Observed Dances	43	38	33	37	34	30	32	49	296
Forager Station:									
Forager Visits	48	43	34	38	39	29	39	49	319
Recruits	4	4	7	2	2	1	3	14	37
Weather:									Averages
Wind Direction	145°	160°	171°	168°	148°	140°	166°	169°	157°
Wind Speed (mph)	0.6	0.6	0.6	0.5	0.7	0.5	1.2	2.0	0.8
Sky Condition	Cdy	Cdy	Cdy	Cdy	Cdy	Cdy	Cdy	Cdy	Cdy
Pressure (mmHg)	770.8	770.8	770.9	770.9	771.0	771.0	771.0	771.0	770.9
Rel. Humidity (%)	58	60	60	60	60	60	60	61	60
Temperature (°C)	20	21	21	21	21	21	21	22	21

Table XII. Results of Experiment 1 (Closer Distance Array). The experiment was performed on June 27, 1974. The experimental scent was peppermint. The recruit distribution is shown in Fig. 46.

"Int." is the Intermediate Station at 42-1/2°.

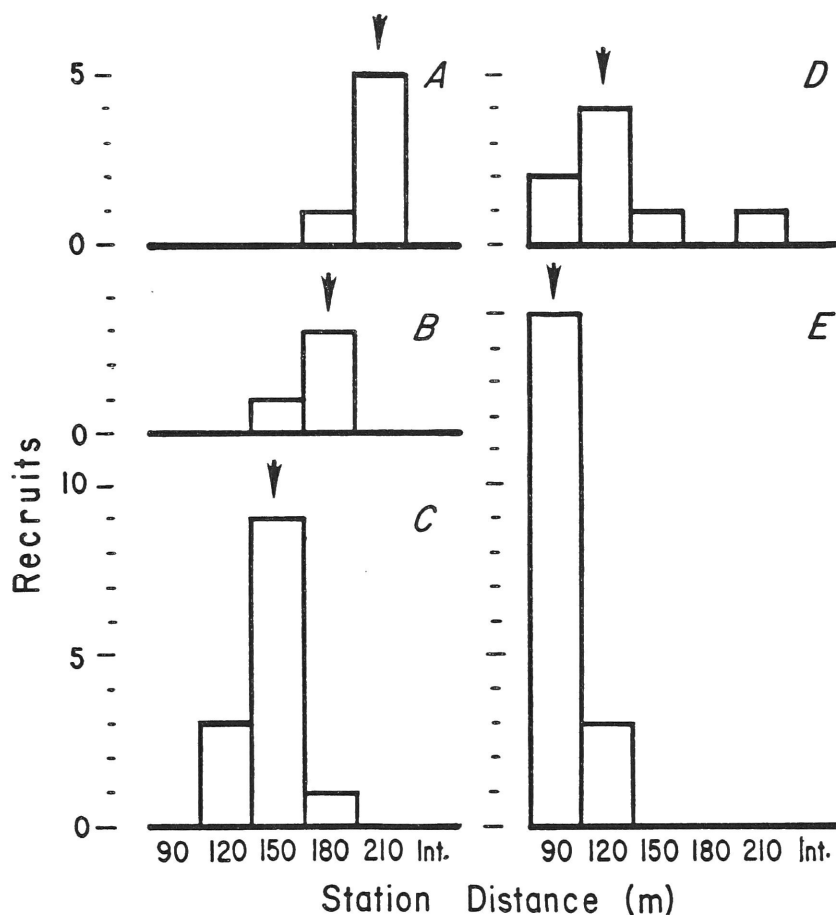


Fig. 47. Recruit Distribution in Experiment 3 (Closer Distance Array). The distance of the Forager Station is indicated by the arrows. The Forager Station was at (A) 210 m for 20 minutes, at (B) 180 m for 10 minutes, at (C) 150 m for 20 minutes, at (D) 120 m for 10 minutes, and at (E) 90 m for 20 minutes. Recruits favored the Recruit Station at the distance indicated by the dances. For additional details, see text and Table XIII.

Table XIII

Time (EDT)		9:10	9:20	9:30	9:40	9:50	10:00	10:10	10:20	Totals
Dance Direction	Distance	87°	85°	86°	85°	85°	86°	86°	86°	
		<u>210m</u>	<u>210m</u>	180m	<u>150m</u>	<u>150m</u>	120m	<u>90m</u>	<u>90m</u>	
Recruits at Recruit Stations	90m	0	0	0	0	0	2	9	6	17
	120m	0	0	0	1	2	4	3	0	10
	150m	0	0	1	3	6	1	0	0	11
	180m	1	0	3	1	0	0	0	0	5
	210m	2	3	0	0	0	1	0	0	6
	Int.	0	0	0	0	0	0	0	0	0/49
Observed Dances		8	14	12	12	11	8	9	14	84
Forager Station:										
Forager Visits		11	15	9	13	14	7	10	18	
Recruits		1	0	2	1	0	3	5	8	
Weather:										Averages
Wind Direction		005°	002°	358°	003°	003°	005°	004°	013°	004°
Wind Speed (mph)		4.1	4.7	6.4	5.8	6.7	7.4	7.4	6.6	6.2
Sky Condition		PC	PC	PC	PC	PC	PC	PC	PC	PC
Pressure (mmHg)		763.3	763.2	763.2	763.3	763.3	763.3	763.3	763.3	763.3
Rel. Humidity (%)		77	77	73	73	73	69	69	69	73
Temperature (°C)		22	22	22	23	23	23	23	23	23

Table XIII. Results of Experiment 3 (Closer Distance Array). The experiment was performed on July 15, 1974. The experimental scent was chamomile. The recruit distribution is shown in Fig. 47.

Longer-Distance Experiments

In order to test the distance accuracy at greater distances, the array was moved to the north so that the array of stations ran from 240 m to 390 m (Fig. 48). The Forager and Control Stations were set out on a line 45° east of the array of Recruit Stations. The light was placed 45° to the right of vertical to direct recruits to the array. The Forager Station was moved to 240 m (10 min.), 270 m (30 min.), 300 m (5 min.), 330 m (5 min.), and 390 m (10 min.) in one experiment (Fig. 49; Table XIV); and in the order 390 m (10 min.), 330 m (5 min.), 300 m (5 min.), 270 m (30 min.), and 240 m (10 min.) in the other (Fig. 50; Table XV). As before, recruits showed a preference for the distance indicated in the dance.

Distance Accuracy

The accuracy of recruits in the distance experiments is shown in Figure 51. These values -- 10.9% at longer distances, and $\pm 12.1\%$ at shorter ones -- can be compared with those from von Frisch's step experiments (Fig. 9) -- $\pm 7.5\%$ when the recruits at the Forager Station are included, or $\pm 14\%$ when they are not. (Up to 1 km the mean error was 20.4%; beyond 1 km it was 9.7%. When recruits at the Forager Station are counted, these numbers become 9.4% and 5.8%.) Again, however, the experiments are not strictly comparable. Von Frisch's Forager Station was located in the middle of the array. His Recruit Stations offered no hive or scent gland odor and no visual landing encouragement.

Effects of von Frisch Techniques

In order to examine the effects of von Frisch's techniques on the apparent accuracy of recruits in step experiments, the experiment was repeated with the Forager Station in the array (Fig. 52) at 315 m. The light was placed in the "up" position so that no misdirection was created. Again, the Recruit Stations were modified to prevent recruits from feeding, allowing only their counting and escape. Since there was no cage of anaesthetized foragers, the Recruit Stations contained no hive odor. Recruits arriving at the Forager Station were captured. The results (Fig. 53; Table XVI) indicate, as expected, that recruits favored the stations near (and ahead of) the Forager Station. The mean recruit accuracy was $\pm 9.0\%$ when

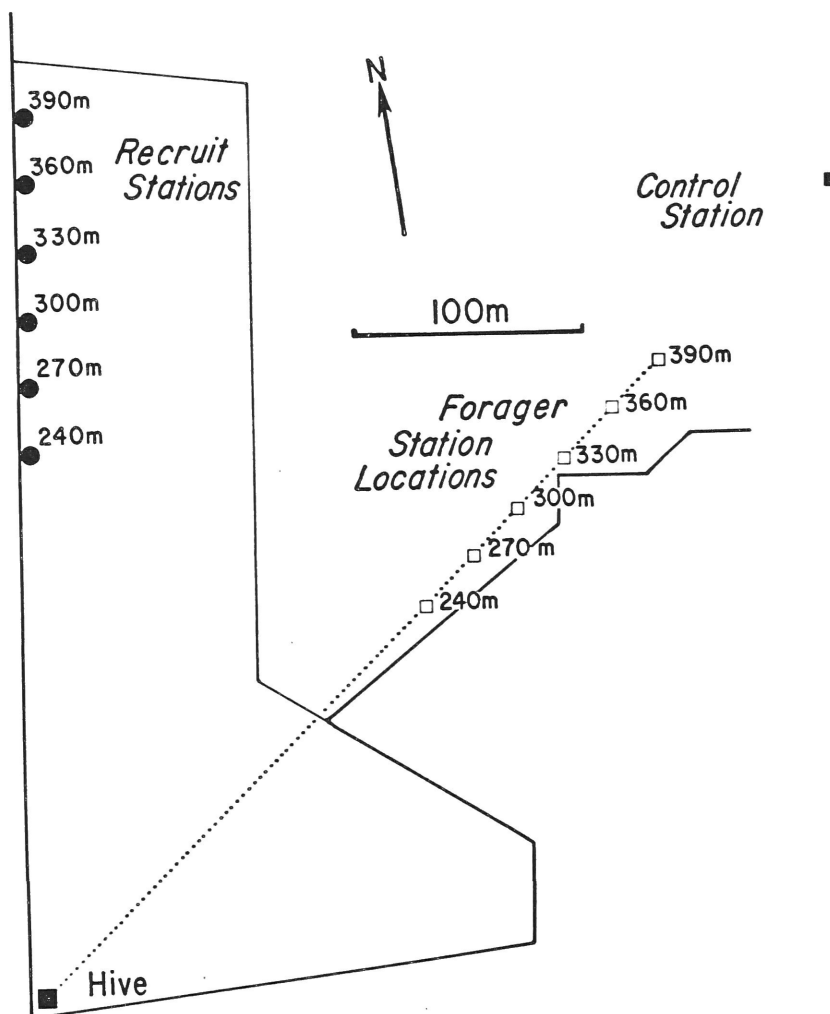


Fig. 48. Farther Distance Array. Ocelli-painted foragers were trained to the northeast to the Forager Station. Control foragers were trained to the Control Station located 500 m from the hive. Recruit Stations were set out at 30 m intervals from 240-390 m on a line 45° to the left of the Forager Station. A light shining on the hive directed recruits to the array of Recruit Stations. From time to time the Forager Station was moved to a different distance from the hive. Recruits favored the Recruit Station at the same distance as the Forager Station (Figs. 49 and 50). For particulars, see text and Tables XIV and XV.

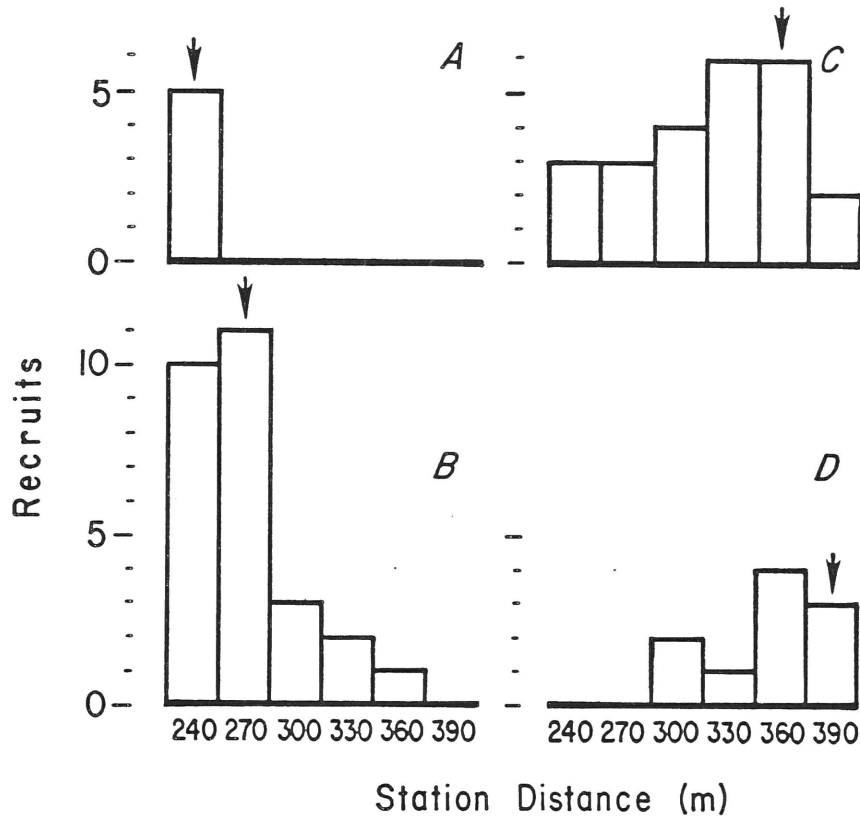


Fig. 49. Recruit Distribution in Experiment 5 (Farther Distance Array). The distance of the Forager Station is indicated by the arrows. The Forager Station was at (A) 240 m for 10 minutes, at (B) 270 m for 30 minutes, at (C) 360 m for 30 minutes, and at (D) 390 m for 10 minutes. Recruits favored the Recruit Station at the distance indicated by the dances. For additional details, see text and Table XIV.

Table XIV

Time (EDT)		8:10	8:20	8:30	8:40	8:50	9:00	9:10	9:20	9:30	Totals
Dance Direction	Distance	42°	45°	45°	44°	47°	46°	44°	45°	43°	
		240m	270m	270m	270m	315m	360m	360m	360m	390m	
Recruits at Recruit Stations	240m	5	2	4	4	2	2	0	1	0	20
	270m	0	4	5	2	0	1	1	1	0	14
	300m	0	1	2	0	3	1	0	3	2	12
	330m	0	2	0	0	2	1	2	3	1	11
	360m	0	0	1	0	0	4	0	2	4	11
	390m	0	0	0	0	0	1	1	0	3	5/7:
Observed Dances		9	15	18	16	22	21	17	17	18	153
Forager Station:											
Forager Visits		16	19	18	21	21	19	22	20	17	173
Recruits		2	0	1	3	1	1	2	2	1	13
Weather:											Averages
Wind Direction		184°	186°	169°	185°	180°	170°	177°	189°	205°	183°
Wind Speed (mph)		0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Sky Condition		PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Pressure (mmHg)		769.0	769.0	769.0	768.9	768.9	768.9	768.9	768.9	768.9	768.9
Rel. Humidity (%)		74	74	69	69	65	66	66	66	66	69
Temperature (°C)		23	23	23	24	24	24	24	24	25	24

Table XIV. Results of Experiment 5 (Farther Distance Array). The experiment was performed on July 23, 1974. The experimental scent was jasmine absolute. The recruit distribution is shown in Fig. 49.

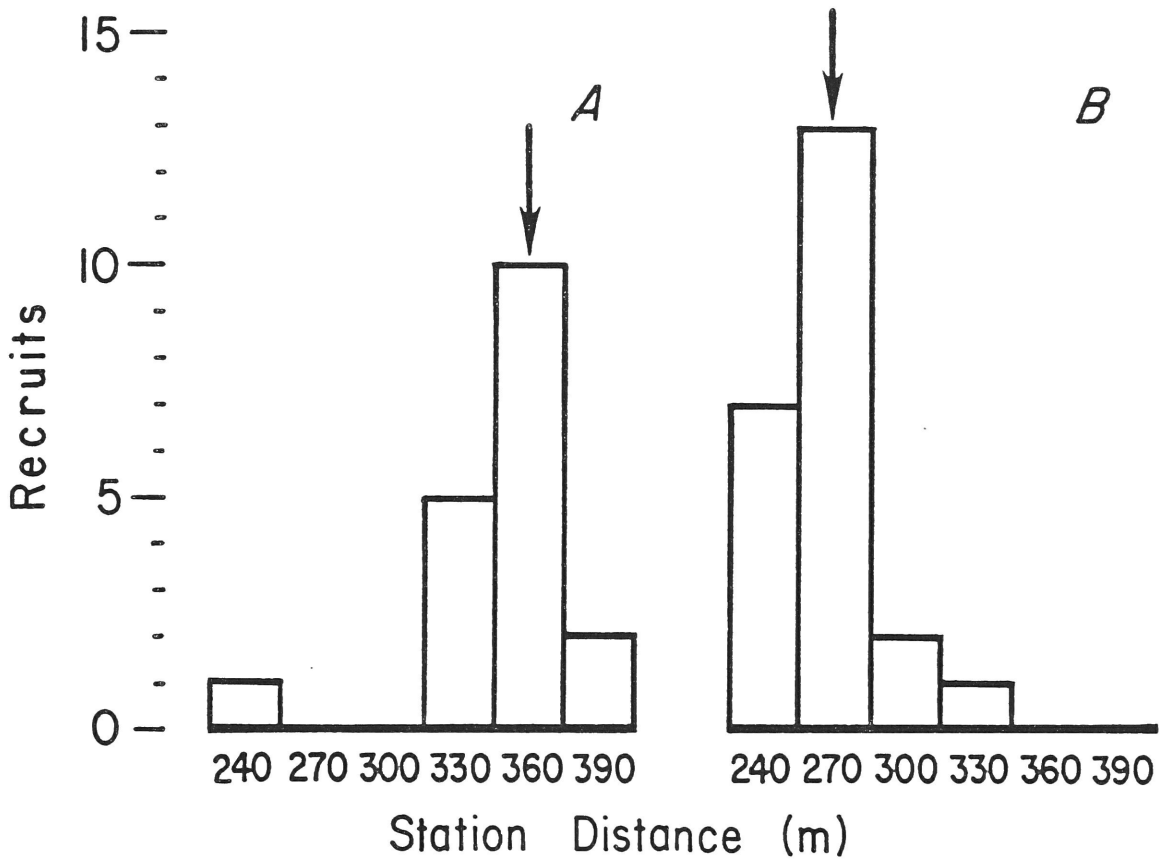


Fig. 50. Recruit Distribution in Experiment 6 (Farther Distance Array). The distance of the Forager Station is indicated by the arrows. The Forager Station was at (A) 390 m for 10 minutes, at (B) 360 m for 30 minutes, at (C) 270 m for 30 minutes, and at (D) 240 m for 10 minutes. Recruits favored the Recruit Station at the distance indicated by the dances. For additional details, see text and Table XV.

Table XV

Time (EDT)		9:00	9:10	9:20	9:30	9:40	9:50	10:00	10:10	10:20	Totals
Dance Direction		45°	45°	45°	49°	44°	44°	43°	44°	44°	
Distance		390m	360m	360m	360m	315m	270m	270m	270m	240m	
Recruits at Recruit Stations	240m	1	1	0	0	0	2	3	2	8	17
	270m	0	0	0	0	1	4	2	7	0	14
	300m	1	0	0	0	2	0	1	1	1	5
	330m	0	3	1	1	1	1	0	0	0	7
	360m	1	3	4	3	1	0	0	0	0	12
	390m	1	0	2	0	0	0	0	0	0	3/58
Observed Dances		6	16	15	21	20	16	14	22	20	148
Forager Station:											
Forager Visits		14	17	18	23	20	18	19	26	24	179
Recruits		0	1	0	1	1	2	1	2	4	12
Weather:											Averages
Wind Direction		160°	173°	178°	180°	171°	172°	168°	170°	147°	166°
Wind Speed (mph)		2.1	2.2	3.4	3.7	4.4	4.0	2.8	2.3	3.3	3.5
Sky Condition		Clr	Clr	Clr	PC	PC	PC	PC	PC	PC	PC
Pressure (mmHg)		762.8	762.8	762.8	762.8	762.8	762.8	762.8	762.8	762.8	762.8
Rel. Humidity (%)		83	83	83	79	79	79	83	87	87	83
Temperature (°C)		25	26	26	26	26	26	26	25	26	26

Table XV. Results of Experiment 6 (Farther Distance Array). The experiment was performed on July 29, 1974. The experimental scent was lavender. The recruit distribution is shown in Fig. 50.

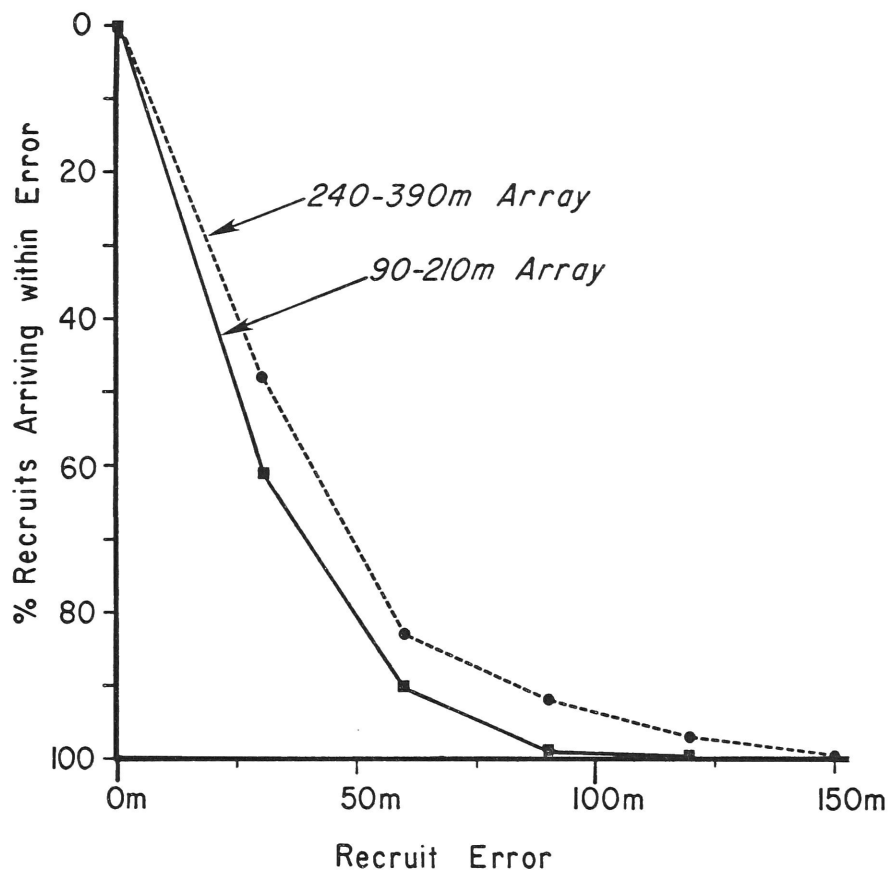


Fig. 51

Fig. 51. Distance Accuracy of Recruits. Recruit accuracy for the "closer" and "farther" distance arrays is plotted. "Recruit error" is taken as the distance from the "target" specified by the dancing. These values may be compared (with caution) to those from von Frisch's step experiments (Fig. 9). As will be demonstrated later, von Frisch's techniques increase the apparent accuracy of recruits. It should also be noted that this data is for a one-dimensional array of stations, whereas searching honey bee recruits are distributed in two dimensions. As will be discussed later, the actual accuracy of recruits may be less than this figure suggests.

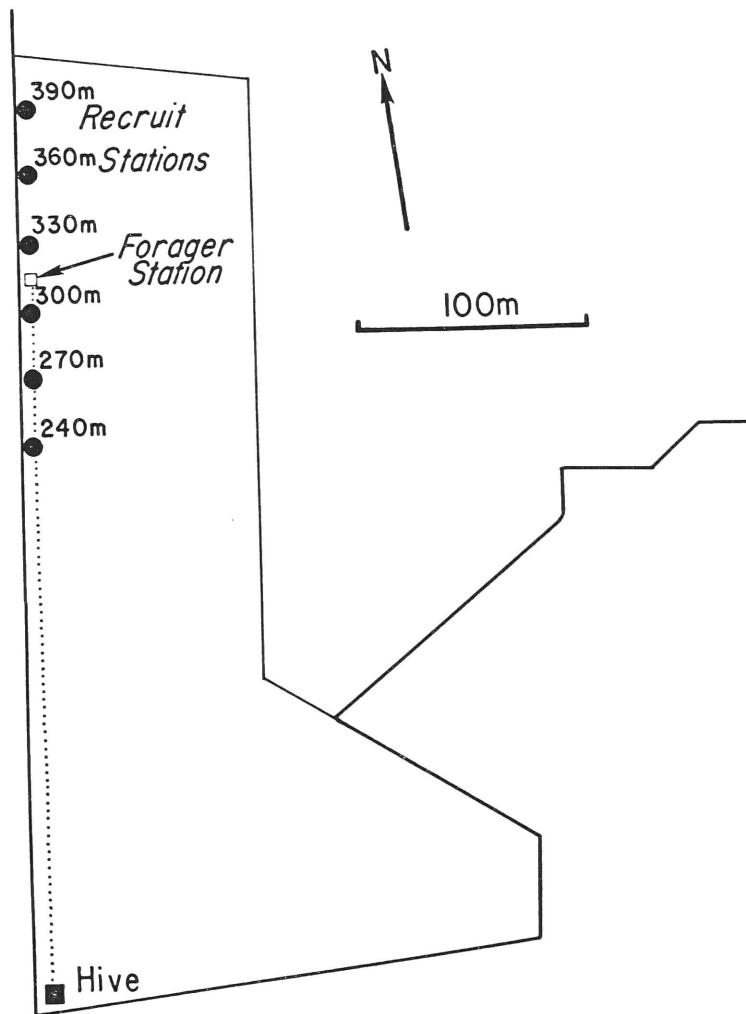


Fig. 52

Fig. 52. Von Frisch Distance Control Array I. Ocelli-painted foragers were trained to the north to the Forager Station located 315 m from the hive. The Recruit Stations were set out at 30 m intervals in the same direction, 240-390 m from the hive. (In von Frisch's experiments, the Recruit Station interval was far larger. The Forager Station was located up to 4400 m from the hive and 50 m from the nearest Recruit Station.) Unlike previous experiments, the Recruit Stations were modified so that entering recruits could not feed. The design also allowed recruits to escape quickly, just as in von Frisch's step experiments. These stations also were without anaesthetized foragers to provide hive and bee odors. The light was placed in the "up" position so that the dances signalled the actual direction of the Forager Station. The recruit distribution is shown in Fig. 53.

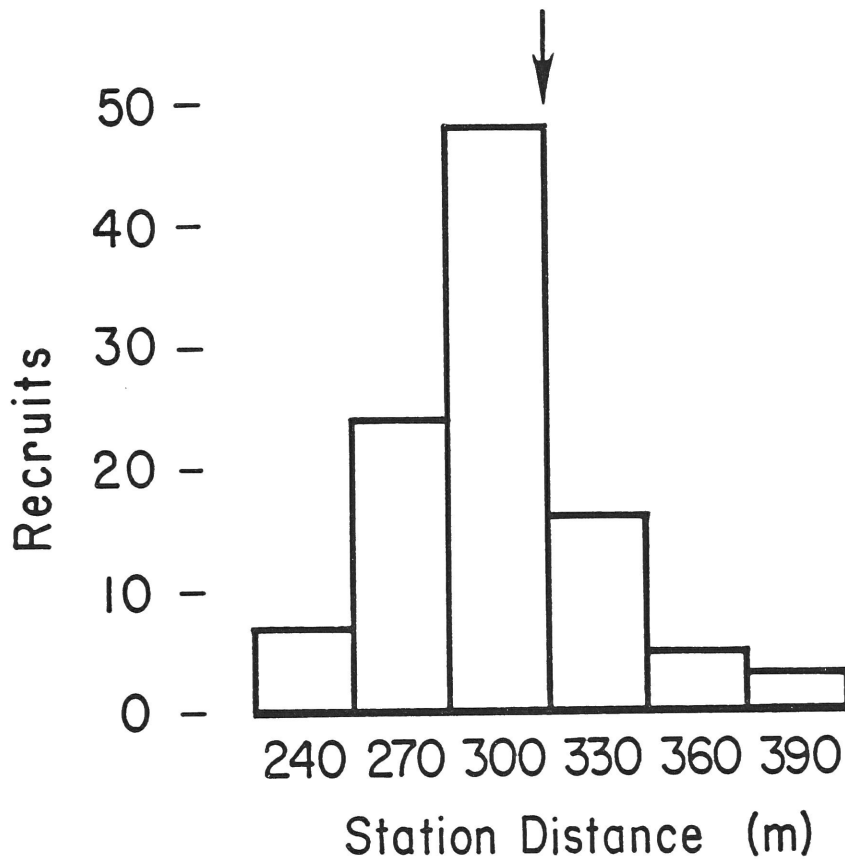


Fig. 53. Recruit Distribution in Experiment 11 (von Frisch Distance Control I). The Forager Station was at 315 m (as indicated by the arrow). During the 40 minutes of the experiment the recruits favored the Forager Station (see Table XVI) and the Recruit Station just downwind at 300 m. For additional details, see text and Table XVI.

Table XVI

Time (EDT)		9:00	9:10	9:20	9:30	Totals
Dance Direction Distance		0° 315m	-3° 315m	0° 315m	1° 315m	
Recruits at Recruit Stations	240m	0	4	1	2	7
	270m	4	5	7	8	24
	300m	12	9	12	15	48
	330m	5	3	3	5	16
	360m	2	1	1	1	5
	390m	1	1	1	0	3/103
Observed Dances		8	18	14	14	54
Forager Station:						
Forager Visits		14	17	17	18	
Recruits		5	9	10	22	
Weather:						Averages
Wind Direction		195°	201°	200°	174°	192°
Wind Speed (mph)		3.4	1.8	2.3	3.2	2.7
Sky Condition		Clr	Clr	Clr	Clr	Clr
Pressure (mmHg)		763.7	763.7	763.7	763.7	763.7
Rel. Humidity (%)		78	74	74	71	75
Temperature (°C)		24	25	24	26	25

Table XVI. Results of Experiment 11 (von Frisch Distance Control I).

The experiment was performed on August 5, 1974. The experimental scent was chamomile. The recruit distribution is shown in Fig. 53.

the recruits at the Forager Station are counted, or $\pm 6.2\%$ when they are excluded. Considering the data in either way, von Frisch's techniques have significant effects on recruit accuracy.

In order to discover whether von Frisch's techniques affect recruit distribution in any other way, the experiment was repeated with the Forager Station located 45° to the right of the array of Recruit Stations, 390 m from the hive (Fig. 54). This time, the 240 m station was odor baited with anaesthetized foragers and loaded with CO. Hence, recruits entering the 240 m station were captured as in earlier experiments. Recruits entering any of the other stations -- not odor baited -- were counted, but could not feed or be captured. The light in the hive was placed 45° to the right of vertical to direct recruits to the recruit array to the north. The Forager Station was moved to 360 m for 30 minutes, then moved to 270 m for the same period. The results are shown in Figure 55 (Table XVII). The presence of forager odor in the array appears to have distorted, but not obscured, the preference of recruits for the distance indicated by the dance.

Effects of Wenner Techniques

In order to examine the effects of Wenner's training technique on distance communication, foragers were trained on a 2 M ylang ylang-scented sucrose solution to a location 240 M to the north (Fig. 48). The same concentrated solution with the same scent used during training was employed during the experiment. The light was placed 85° to the left of vertical to direct recruits to the array of Recruit Stations to the east. The Forager Station was moved to 180 m for 30 minutes, then, over a period of 10 minutes, to 90 m where it remained for an additional 30 minutes. The distribution of recruits (Fig. 56; Table XVIII) was the same whether the dance signalled 90 m or 180 m. This result is in agreement with Wenner's (1967) work, but in sharp contrast to the data from my misdirection experiments (Figs. 49 and 50) in which the "standard" training technique was used. Wenner's training technique appears to have a serious effect on recruit behavior.

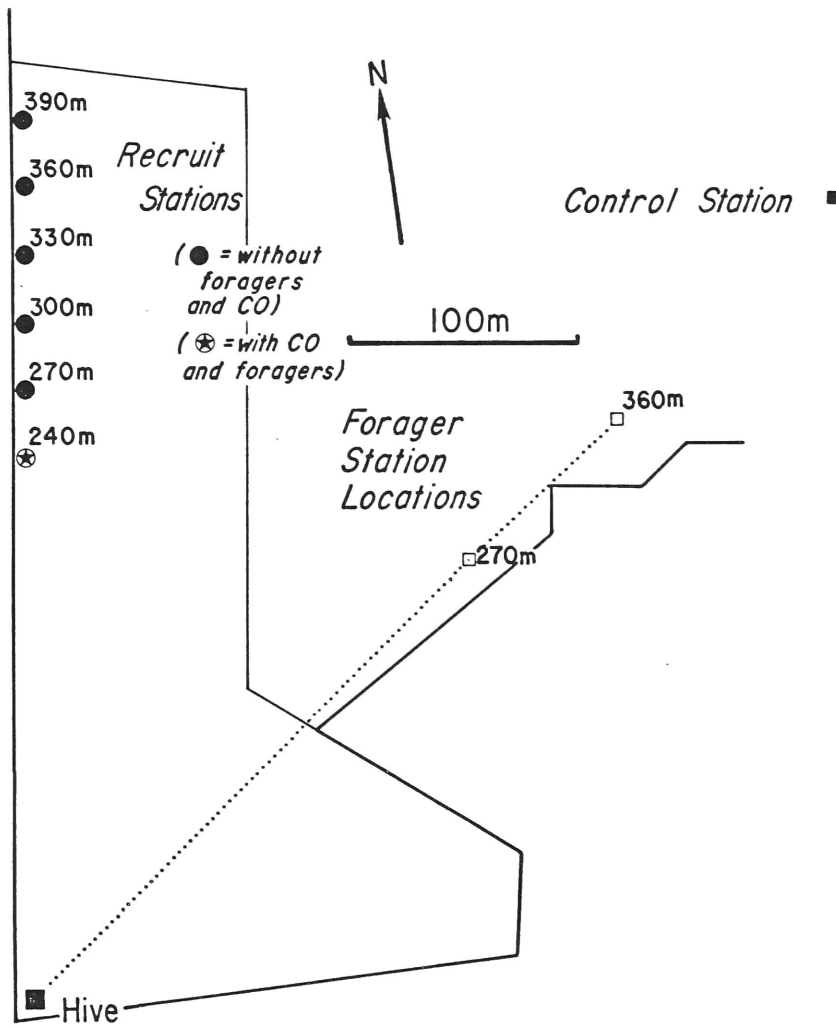


Fig. 54

Fig. 54. Von Frisch Distance Control Array II. Ocelli-painted foragers were trained to the northeast to the Forager Station. Control foragers were trained to the Control Station located 500 m from the hive. Recruit Stations were set out at 30 m intervals from 240-390 m in a line 45° left of the Forager Station. Unlike those in most experiments, the 5 Recruit Stations from 270-390 m were modified as in experiment 11 -- recruits were allowed to escape, but prevented from feeding; in addition, the stations lacked the odor of anaesthetized foragers. The Recruit Station at 240 m, on the other hand, was normal -- that is, baited with anaesthetized foragers and filled with CO. Hence, only recruits arriving at this station were captured. The light shining on the hive was placed to direct recruits to the line of Recruit Stations. The Forager Station was located first at 360 m, then at 270 m. The recruit distribution as shown in Fig. 55.

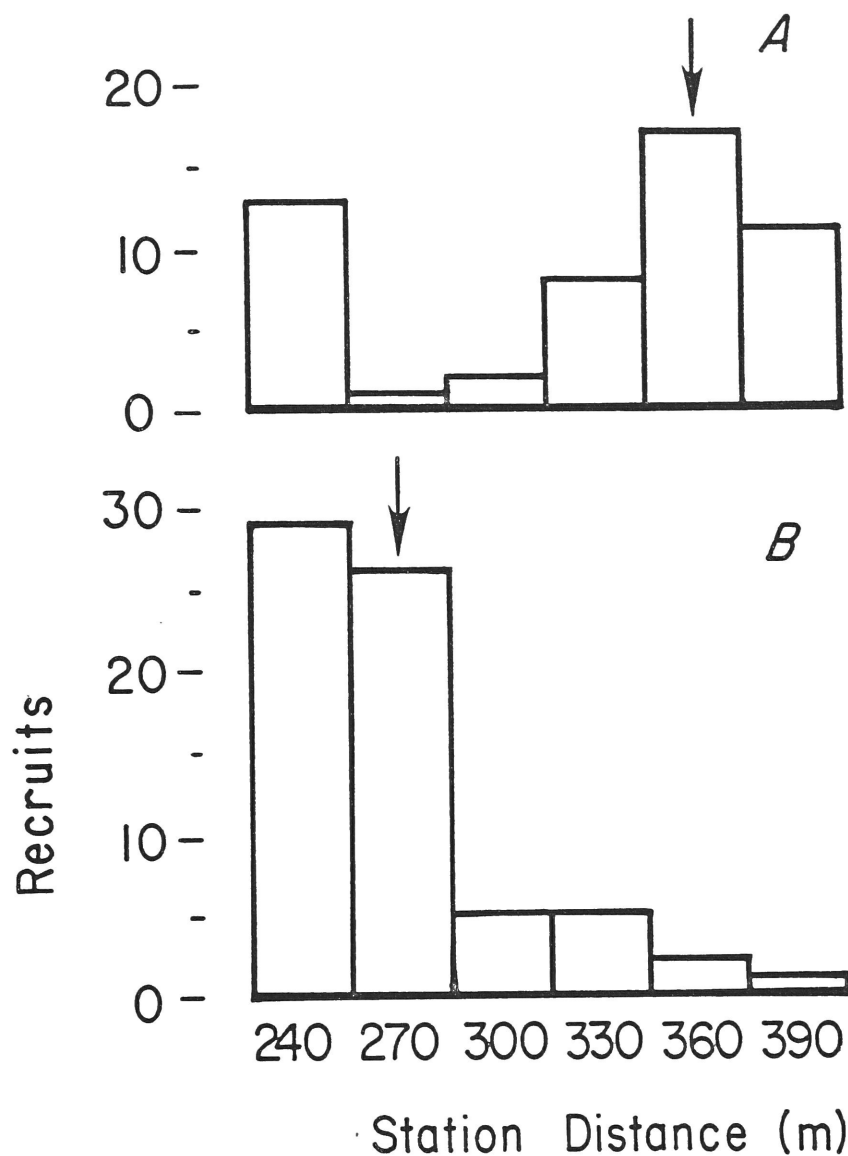


Fig. 55. Recruit Distribution in Experiment 12 (von Frisch Distance Control II). The distance of the Forager Station is indicated by the arrows. Recruits favored both the station baited with forager odor at 240 m and the station at the distance actually indicated by the dance. For additional details, see text and Table XVII.

Table XVII

Time (EDT)		9:30	9:40	9:50	10:00	10:10	10:20	Totals
Dance Direction		47°	42°	43°	43°	45°	44°	
Distance		360m	360m	360m	270m	270m	270m	
Recruits at Recruit Stations	240m	7	2	4	9	9	11	42
	270m	1	0	0	7	6	13	27
	300m	1	1	0	1	1	3	7
	330m	2	4	2	2	1	2	13
	360m	5	7	5	2	0	0	19
	390m	6	2	3	0	1	0	12/120
Observed Dances		11	17	20	20	16	17	101
Forager Station:								
Forager Visits		13	18	22	16	19	20	
Recruits		2	4	2	3	1	2	
Weather:								Averages
Wind Direction		222°	188°	174°	167°	166°	193°	188°
Wind Speed (mph)		1.4	1.1	1.3	1.2	1.4	2.1	1.4
Sky Condition		Clr	Clr	Clr	Clr	Clr	Clr	Clr
Pressure (mmHg)		768.6	768.7	768.7	768.7	768.7	768.7	768.7
Rel. Humidity (%)		77	77	77	72	72	69	74
Temperature (°C)		22	22	22	22	22	22	22

Table XVII. Results of Experiment 12 (von Frisch Distance Control II).

The experiment was performed on August 6, 1974. The experimental scent was geranium bourbon. The recruit distribution is shown in Fig. 55.

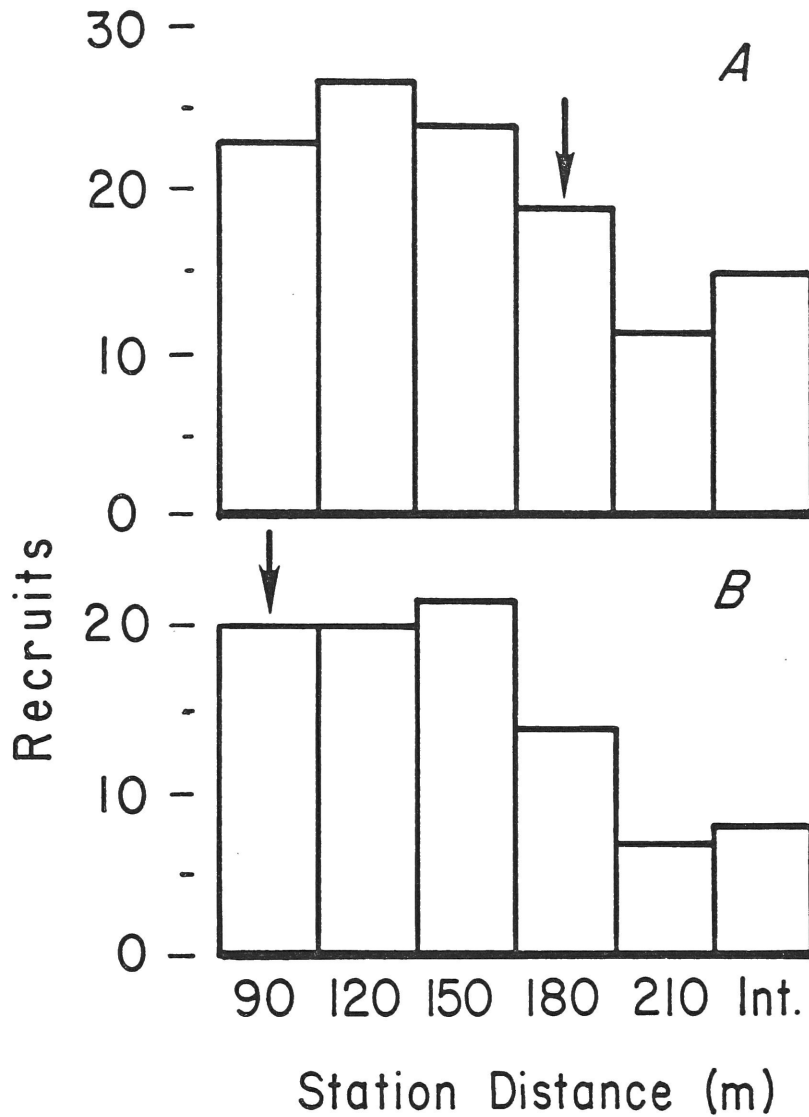


Fig. 56. Recruit Distribution in Experiment 18 (Wenner Distance Control). After training according to Wenner's technique, the Forager Station was placed at (A) 180 m for 30 minutes, then moved to (B) 90 m for 30 minutes (as indicated by the arrows). Recruits under these conditions displayed no preference for the distance indicated by the dance. For additional details, see text and Table XVIII.

Table XVIII

Time (EDT)		9:30	9:40	9:50	10:00	10:10	10:20	10:30	Totals
Dance Direction	Distance	88° 180m	86° 180m	86° 180m	87° 135m	86° 90m	86° 90m	85° 90m	
Recruits at Recruit Stations	90m	8	4	11	10	7	9	4	53
	120m	13	8	6	5	7	11	2	52
	150m	10	6	8	8	11	9	2	54
	180m	8	6	5	3	5	7	2	36
	210m	3	3	5	1	5	1	1	19
	Int.	4	6	5	6	1	5	2	29/243
Observed Dances		6	9	12	14	14	15	13	83
Forager Station:									
Forager Visits		20	23	18	15	13	22	20	
Recruits		9	10	10	7	8	18	15	
Weather:									Averages
Wind Direction		195°	185°	182°	184°	184°	193°	184°	187°
Wind Speed (mph)		1.1	1.2	1.3	1.2	1.1	1.4	1.1	1.2
Sky Condition		PC	PC	PC	PC	PC	PC	PC	PC
Pressure (mmHg)		766.7	766.7	766.7	766.7	766.7	766.7	766.7	766.7
Rel. Humidity (%)		74	74	74	70	70	70	67	71
Temperature (°C)		25	24	24	24	24	24	26	24

Table XIII. Results of Experiment 18 (Wenner Distance Control).
 The experiment was performed on August 13, 1974.
 The experiment scent was ylang ylang. The recruit distribution is shown in Fig. 56. The DC power to the Recruit Stations failed shortly after 10:30, accounting for the smaller numbers in that column.

INTEGRATION OF SEPARATE DANCES

As described earlier, Wenner, Wells, and Johnson (1969) performed an experiment in which foragers frequented two stations with experimental scent, 90° apart (Fig. 15). On subsequent days the scent was removed from the food and a third station with scented food was established between the Forager Stations. Recruits favored the Center Station, ignoring the stations indicated by the dancing. This experiment was repeated using the misdirection technique.

Using Wenner's methods, foragers were trained on 2 M orange-scented sucrose to two Forager Stations 150 m from the hive. One station was to the north while the other was placed 30° to the east (Fig. 57). On the next day, Recruit Stations were set out 150 m from the hive at 55°, 70°, and 85° to the east. The Recruit Stations were odor baited in the usual way, but orange scent was added only to the food of the Center (70°) Station. The light in the hive was placed 55° to the left of vertical so that the dances of the two groups of foragers indicated the two Recruit Stations which had no food scent (55° and 85°). The experiment lasted 50 minutes. The results (Fig. 58; Table XIX) confirm the observations of Wenner et al. (1969) that recruits under these circumstances favor the scented, middle station.

Lindauer (1971) suggested that the preference for the middle might occur because individual recruits "integrate" the dances to the two end stations and fly out to the average direction. Although simple olfactory recruitment to the odor of orange scent in the hive seems a more likely explanation, the possibility that recruits might average separate dances was tested. Since honey bees clearly average separate dance cycles (von Frisch and Jander 1957) and indirect flight paths (von Frisch 1967a, pp. 173-186), they could be capable of averaging different dances. On the other hand, the dances averaged would be separated in time by several minutes since recruits typically attend one dance, fly out for 6 minutes, and then return to attend another (Esch and Bastian 1970; Mautz 1971; Johnson and Wenner 1970). Lindauer (1971) feels that his data, the Wenner et al. (1969) results, as well as those of Gould et al. (1970) support the dance integration hypothesis. Neither of the latter groups agrees with his interpretation (Wells and Wenner 1973; Gould et al. unpublished).

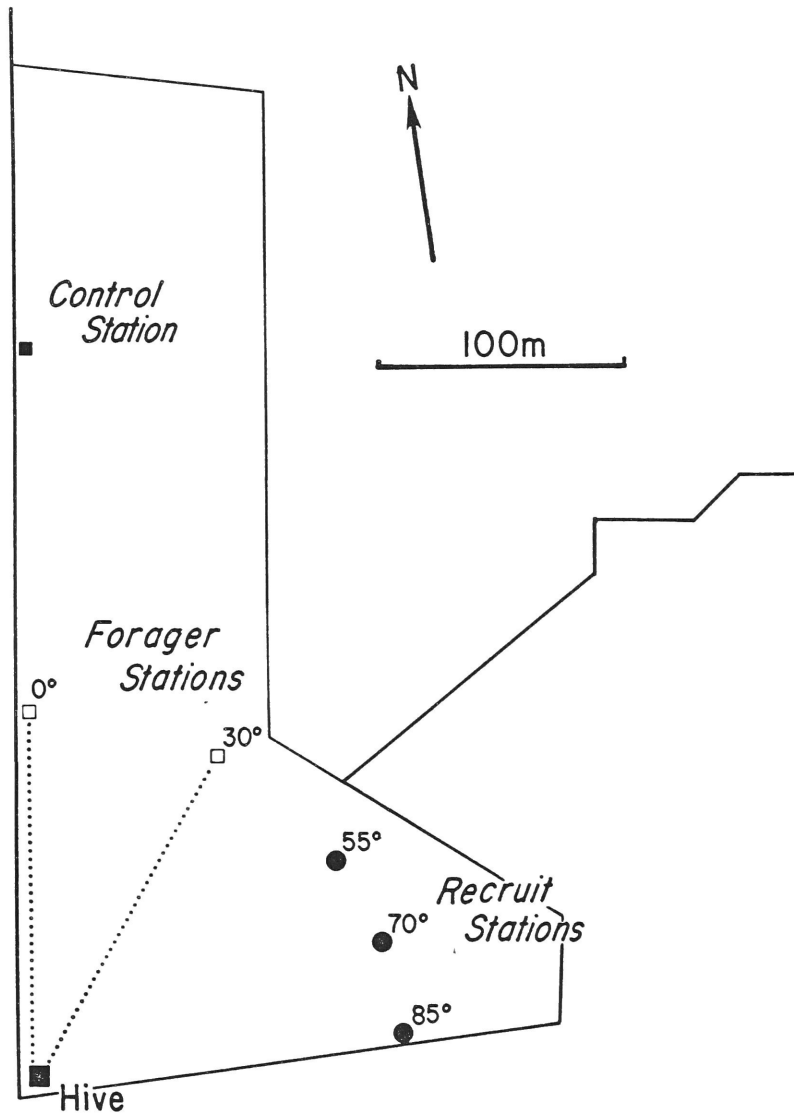


Fig. 57

Fig. 57. Array for Wenner, et al. Control. Two groups of ocelli-painted foragers were trained using Wenner's technique (a concentrated solution containing the experimental scent) to two Forager Stations 30° apart and 150 m from the hive. Control Foragers were trained to the Control Station 300 m to the north. Three Recruit Stations were set out 150 m from the hive at angular intervals of 15° as shown. The experimental odor at the Forager Station was removed. The light shining on the hive was placed 55° to the left of vertical so that dances by the 0° -station foragers indicated the 55° Recruit Station, while those of the 30° -station foragers indicated the 85° Recruit Station. Only the 70° Recruit Station, however, contained the experimental odor. Recruits favored the 70° station, as shown in Fig. 58.

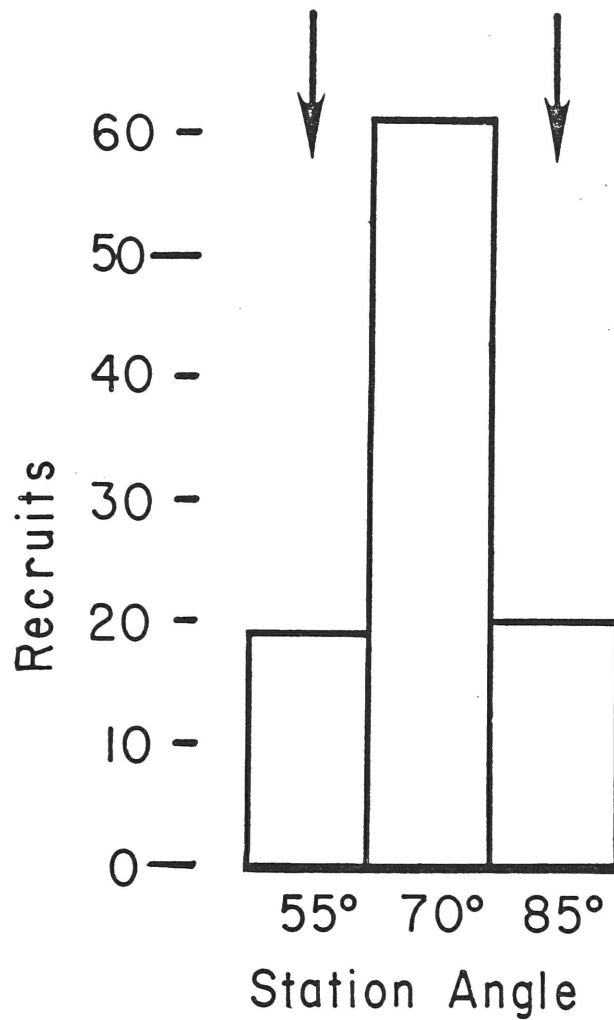


Fig. 58. Recruit Distribution in Experiment 17 (Wenner, et al. Control). Although forager dances indicated the stations without the experimental scent (see arrows) at 55° and 85°, recruits favored the Center Station (at 70°) containing the experimental odor. See text and Table XIX for details.

Table XIX

Time (EDT)		9:00	9:10	9:20	9:30	9:40	Totals
Dance Directions	57°	57°	57°	55°	54°		
	86°	88°	86°	86°	85°		
Recruits at Recruit Stations	55°	2	3	2	4	8	19
	70°	3	7	10	12	29	61
	85°	1	3	5	4	7	20/100
Observed Dances	55°	4	7	8	13	14	46
	85°	1	6	11	11	13	42
Weather:							Averages
Wind Direction	126°	083°	087°	094°	094°		096°
Wind Speed (mph)	1.0	1.9	1.4	0.8	0.8		1.2
Sky Condition	Clr	Clr	Clr	Clr	Clr		Clr
Pressure (mmHg)	770.1	770.1	770.1	770.1	770.1		770.1
Rel. Humidity (%)	65	61	59	65	66		63
Temperature (°C)	23	24	25	23	25		24

Table XIX. Results of Experiment 17 (Wenner, et al. Control). The experiment was performed on August 12, 1974. The experimental scent was sassafrass. Since there were two Forager Stations to be monitored, there is no reliable data on forager visits and recruits to Forager Stations. The recruit distribution is plotted in Fig. 58.

To test whether recruits can integrate separate dances, an array of 5 Recruit Stations was established 150 m from the hive at $7\text{--}1/2^\circ$ intervals (Fig. 59). Two Forager Stations were placed 150 m from the hive. One was set out to the north, while the other was moved as needed from adjacent to the north station to as much as 30° east. The light was placed 58° to the left of vertical to direct recruits to the array of Recruit Stations.

In both of the experiments, the movable Forager Station was first placed adjacent to the fixed Forager Station. After 30 minutes, the movable station ("B") was moved $7\text{--}1/2^\circ$ east every 10 minutes (Fig. 59) until it reached 30° , where it remained for 30 minutes. The fixed station ("A") at 0° did not move. The results are plotted in Figures 60 and 61 (Tables XX and XXI). Many recruits did arrive at the Recruit Stations in the middle of the array. Whether this was due to the normal directional error of two separate groups of recruits, each seeking a single end station, or due instead to a minority seeking some sort of average, is the question. In order to examine this problem more closely, the distributions from the first 30 minutes of each experiment -- a measure of recruit error when seeking a single station -- were summed. This summed distribution was then used to predict the recruit distribution when both end stations were being signalled (Fig. 62). The resulting curve can be compared against the summed results obtained in the last 30 minutes of the experiments when dances to both stations were being performed simultaneously (Fig. 62). If any averaging by recruits were taking place, a larger proportion of the recruits would be expected at the Center Station. The difference between the theoretical and observed distributions is small. Fewer than 1 in 15 recruits could be presumed to be averaging dance directions.

SOME IMPLICATIONS OF THE DATA

Do Recruits Arrive in Groups?

Anecdotal observation suggests that hesitant recruits often land when they see other bees already at a source. As a result, recruits are often scored as arriving in clumps. Whether this hesitancy results from the presence of the human observer, the artificial food source, or normal behavior is another question. Some evidence of this phenomenon was noticed

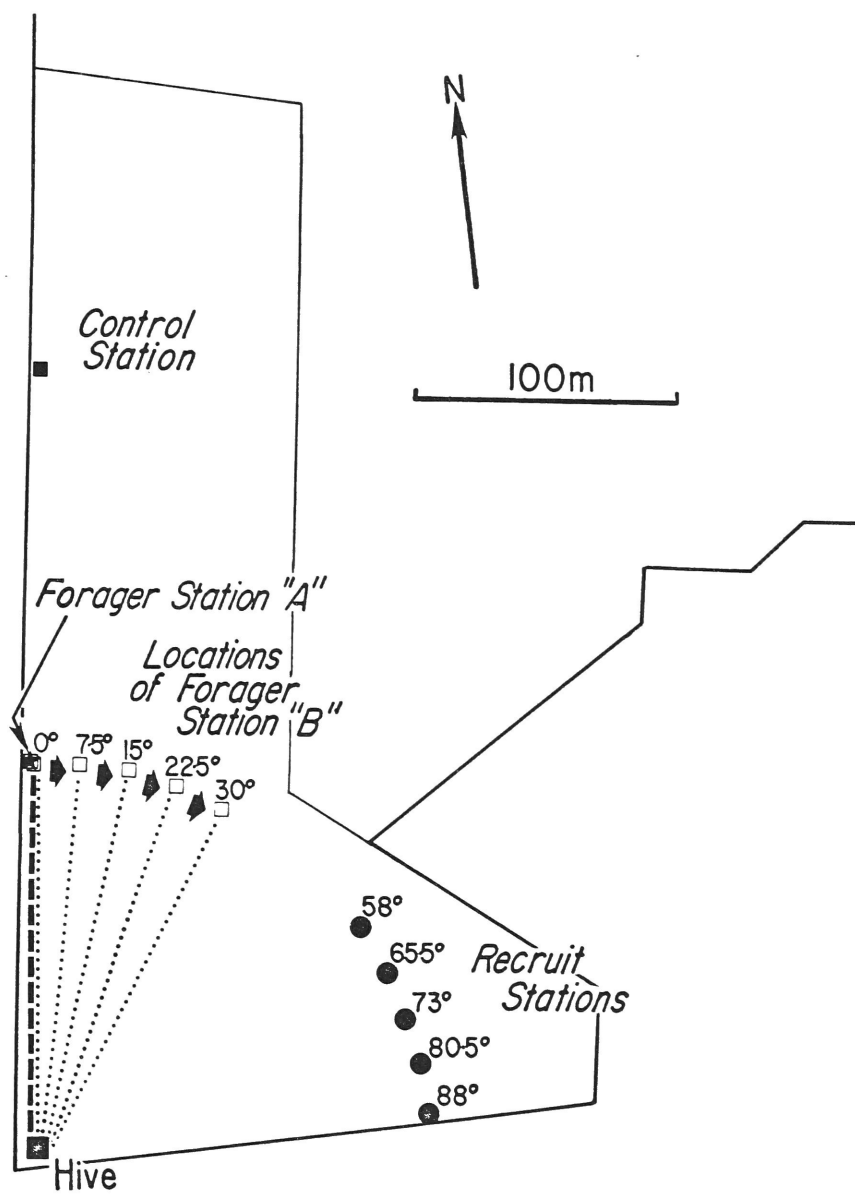


Fig. 59

Fig. 59. Array for Lindauer "Integration" Control. Two groups of ocelli-painted foragers were trained to two Forager Stations 150 m to the north. Control foragers were trained to the Control Station located 300 m from the hive. An array of Recruit Stations was set out 150 m from the hive at $7\text{-}1/2^\circ$ intervals. When the experiment began, the light was placed 58° left of vertical to direct recruits to the 58° Recruit Station. After 20 or 30 minutes, one of the Forager Stations ("B") was moved $7\text{-}1/2^\circ$ to the right every 10 minutes until it reached 30° , where it remained for 40 minutes. At this point the dances of the 0° -station ("A") foragers indicated the 58° Recruit Station, while those of the 30° -station ("B") foragers indicated the 88° Recruit Station. If any integration of dance directions were taking place, an enhancement of recruitment to the middle of the array (73°) would be expected. That is, recruits averaging two dances would, by chance, average two to $58^\circ\ 1/4$ of the time, two to $88^\circ\ 1/4$ of the time, and one to each -- 58° and 88° -- $1/2$ of the time. Thus, twice as many dance-averaging recruits would go to the Center Station as either end. See Figs. 60, 61, and 62, as well as Tables XX and XXI for the results.

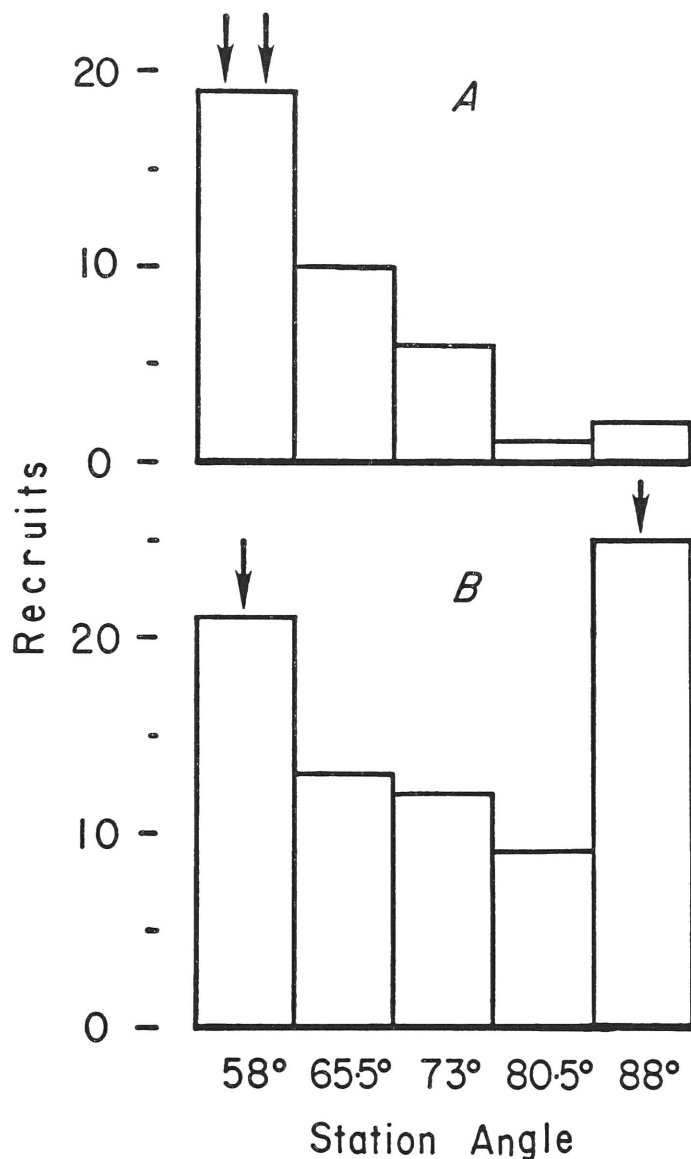


Fig. 60. Recruit Distribution in Experiment 13 (Lindauer Integration Control). (A) When both Forager Stations were at 0°, all of the dancing indicated the 58° Recruit Station (arrow); recruits favored the station being indicated by the dancing. (B) When the Forager Stations were at 0° and 30°, the dances indicated both 58° and 88° (arrows); again, recruits favored the indicated stations. See text and Table XX for additional details.

Table XX

Time (EDT)		8:50	9:00	9:10	9:20	9:30	9:40	9:50	10:00	10:10	Totals
Dance Directions		2° 0°	-3° -2°	-1° 7°	-1° 14°	0° 23°	1° 28°	2° 32°	2° 31°	0° 31°	
Recruits at Recruit Stations	58°	10	9	8	5	6	5	5	6	5	59
	65-1/2°	4	6	6	5	1	4	6	1	2	35
	73°	3	3	3	3	4	3	2	6	1	28
	80-1/2°	1	0	2	2	4	2	3	2	2	18
	88°	1	1	0	2	1	5	6	7	7	35/17
Observed Dances	0°	4	7	8	7	10	13	9	12	10	80
	Movable	8	10	10	12	10	15	10	8	8	91
Weather:											Averages
Wind Direction		356°	339°	0.8°	007°	011°	018°	356°	000°	007°	003°
Wind Speed (mph)		2.3	3.5	2.5	2.0	2.0	3.3	3.7	4.0	2.0	2.8
Sky Condition		PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Pressure (mmHg)		769.5		769.5		769.5		769.5			769.5
Rel. Humidity (%)		81	81	77	78	78	74	71	72	71	76
Temperature (°C)		22	22	22	23	23	24	26	27	26	24

Table XX. Results of Experiment 13 (Lindauer Integration Control).

The experiment was performed on August 8, 1974. The experimental scent was jasmine absolute. Since there were two Forager Stations, no reliable data from those stations could be gathered. The recruit distribution is plotted in Fig. 60.

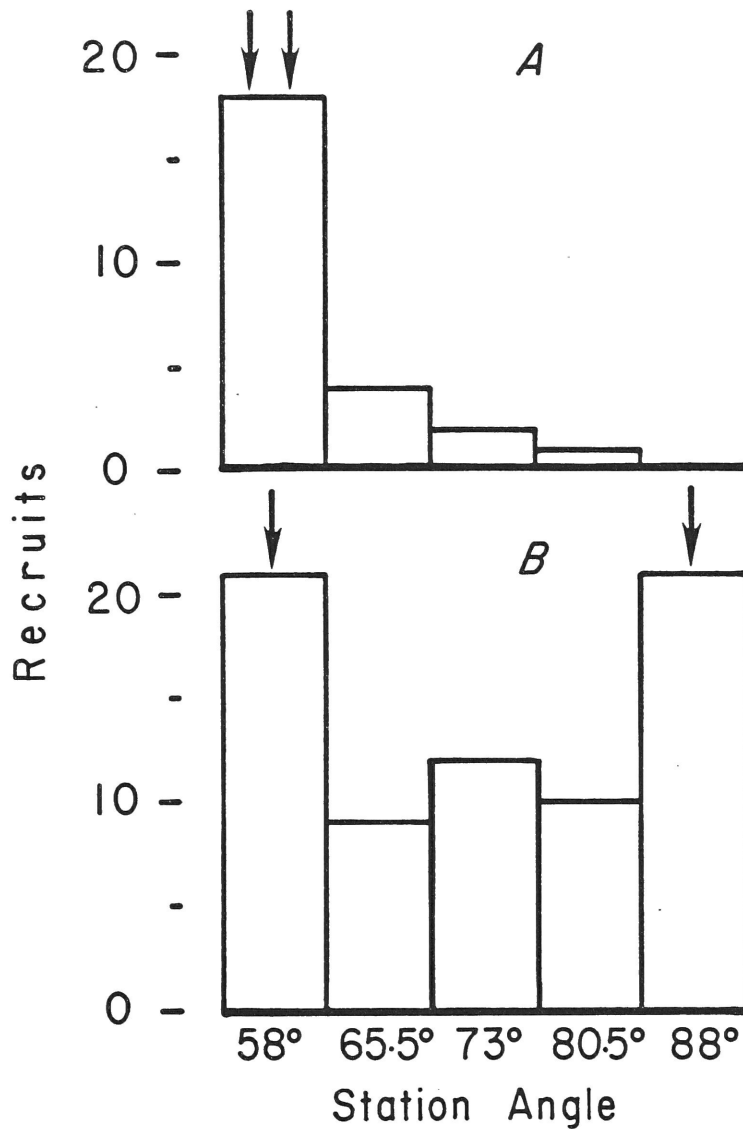


Fig. 61. Recruit Distribution in Experiment 14 (Lindauer Integration Control). (A) When both Forager Stations were at 0°, all of the dancing indicated the 58° Recruit Station (arrow). (B) When the Forager Stations were at 0° and 30°, the dances indicated both 58° and 88° (arrows). This experiment is identical to Experiment 13. See text and Table XXI for additional details.

Table XXI

Time (EDT)		8:40	8:50	9:00	9:10	9:20	9:30	9:40	9:50	10:00	10:10	Totals
Dance Directions		0° 1°	0° -2°	2° 0°	3° 8°	-2° 13°	0° 20°	-1° 27°	-1° 31°	3° 31°	0° 32°	
Recruits at Recruit Stations	58°	7	5	6	8	6	3	6	5	6	4	56
	65-1/2°	1	0	3	3	5	1	4	3	0	2	22
	73°	1	1	0	2	3	4	3	3	3	3	23
	80-1/2°	0	1	0	1	0	4	2	2	2	3	15
	88°	0	0	0	1	0	1	4	6	5	6	23
Dances	0°	6	3	8	11	14	9	12	12	8	6	89
	Movable	3	5	8	9	15	15	11	9	9	8	92
Weather:												Averages
Wind Direction		000°	004°	356°	007°	018°	000°	356°	356°	000°	032°	004°
Wind Speed (mph)		4.3	5.7	5.9	5.2	3.8	4.0	6.0	4.2	2.0	5.0	4.6
Sky Condition		PC	PC	PC	PC	PC	PC	PC	PC	PC	PC	PC
Pressure (mmHg)		768.5	768.5	768.5	768.5	768.5	768.6	768.6	768.6	768.6	768.5	768.5
Rel. Humidity (%)		86	86	81	82	82	78	78	74	74	74	80
Temperature (°C)		21	21	22	22	22	23	24	24	24	25	23

Table XXI. Results of Experiment 14 (Lindauer Integration Control). The experiment was performed on August 9, 1974. The experimental scent was lavender. Since there were two Forager Stations, no reliable data was gathered from these stations. The recruit distribution is shown in Fig. 61.

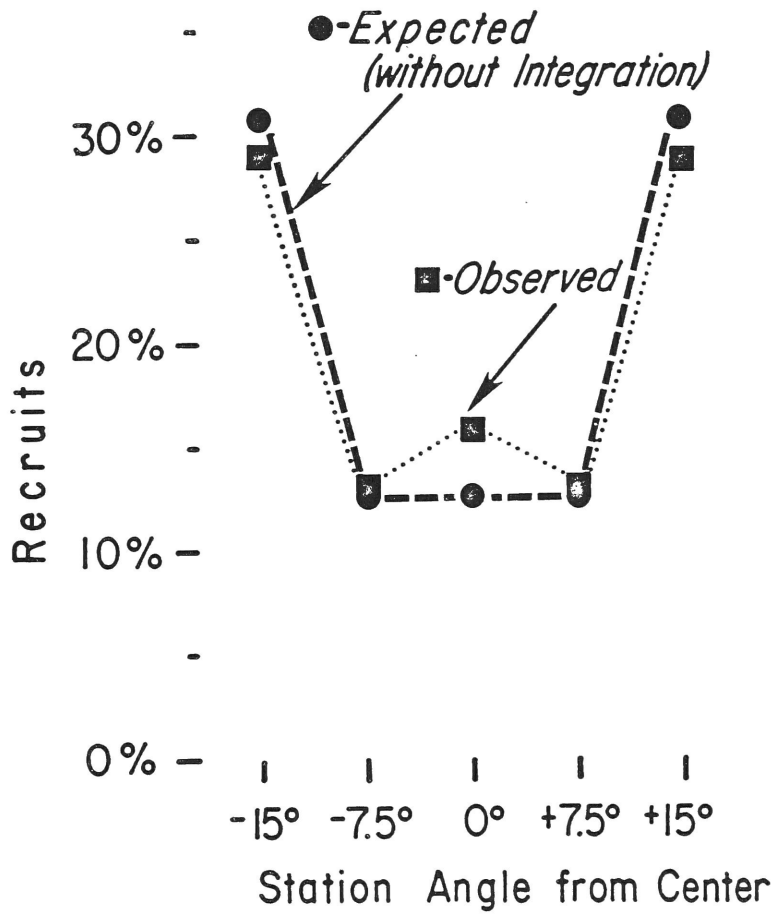


Fig. 62

Fig. 62. Recruit Distribution in Integration Experiments. The results of experiments 13 and 14 are combined to test the Integration hypothesis. The results of the first portion of each experiment are taken as a measure of recruit accuracy under these conditions when a single end station is indicated. To estimate the results to be expected when both end stations are indicated, but no integration of dance directions is taking place, the single-station distribution assuming the $+15^\circ$ station to be the "target" was simply added to the same distribution assuming the -15° station to be the target. The dashed line represents this sum. This curve may be compared with the results actually obtained when both end stations were simultaneously indicated by the dancing -- the final 40 minutes of the two experiments. Any integration of directions should be revealed by an enhancement of recruitment to the Center (0°) Station. In fact, there is only a 6-bee difference between the curves.

upon inspection of the misdirection data -- under conditions which exclude the possibility that the presence of human observers cause the hesitancy. To examine this possibility more closely, the station and arrival time of each recruit in the first 11 experiments was analyzed by computer. The intervals between recruit arrivals at each station were calculated. Figure 63 presents this data.

A substantial enhancement of short recruit arrival intervals is obvious in Figure 63. On the other hand, intervals between recruit arrivals at different stations -- a sort of yoked control in which the arrival of a recruit at one station could not be expected to have any effect at other stations -- showed no enhancement at short intervals. The distribution plotted in Figure 63 could only have resulted from "clumping" or from substantial periods with an arrival rate of at least 10 recruits/minute. Since the highest 10-minute rate ever observed in the first 11 experiments was only 2 recruits/minute, the second possibility is excluded.

Whether recruit hesitancy is normal or an artifact of other experimental conditions remains to be tested.

How Long Do Recruits Take?

The instantaneous shifts of dance directions made possible by the misdirection technique allow an indirect calculation of the time which recruits require to find a food source. Assuming a constant recruitment rate, the increase in arrival rate at a newly signalled station from some background to a maximum level must reflect how long recruits take to get from the dance to the target.

Recruit arrival times were analyzed by computer for experiments 1-6 and 13-14. The results were assigned to one-minute intervals and plotted both when dances started and stopped indicating a particular station. From the data of Gould et al. (1970 and unpublished), Esch and Bastian (1970), and Mautz (1971), the search times, and hence the delay until the maximum level is reached, are expected to be on the order of 10-15 minutes. The data from the misdirection experiments (Fig. 64, left curve) suggest that the interval may be considerably smaller. The experiments are not strictly comparable, however, since in the earlier work only one station was

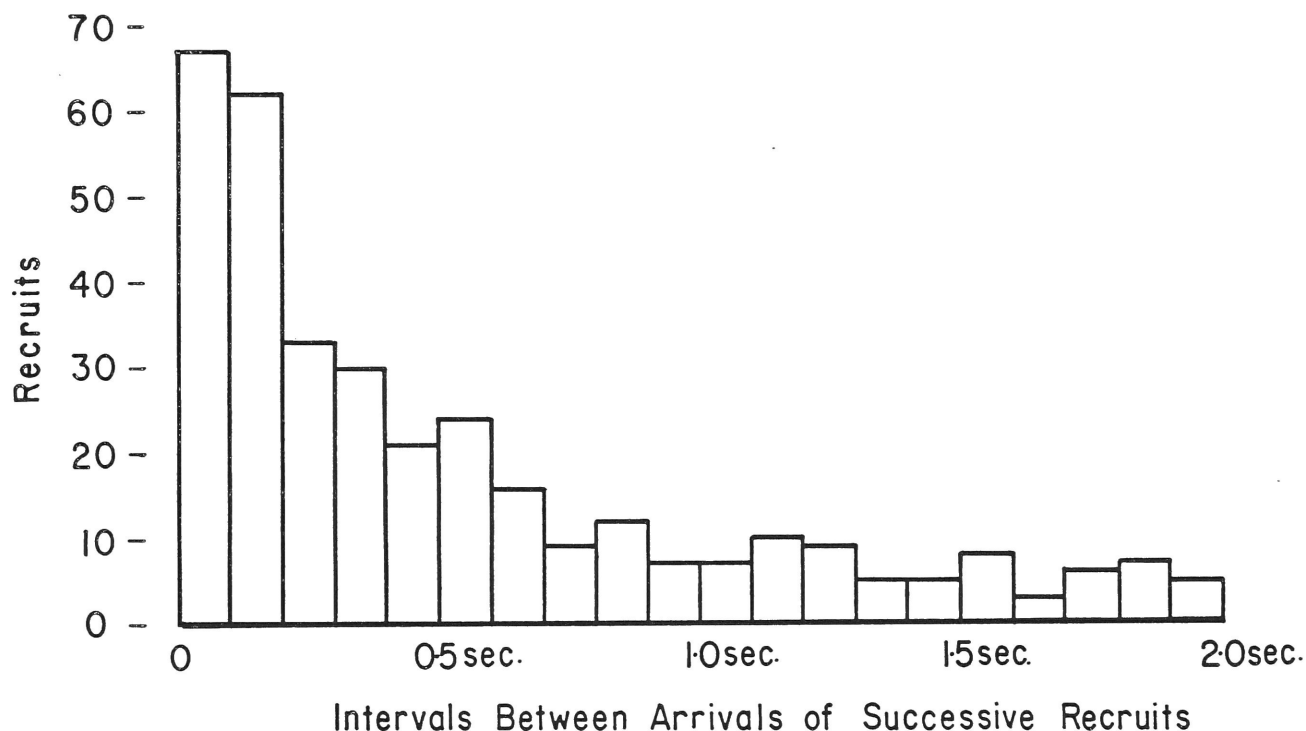


Fig. 63. Recruit Arrival Intervals. The intervals between the arrivals of subsequent recruits at particular stations are plotted in this histogram from experiments 1-10. The total number of intervals was 1135. A substantial enhancement of short intervals is obvious. This enhancement cannot be explained on the basis of the low recruitment rate, and must therefore reflect the tendency of recruits to land together. The between-station intervals each had 6-7 recruits and no enhancement at short intervals.

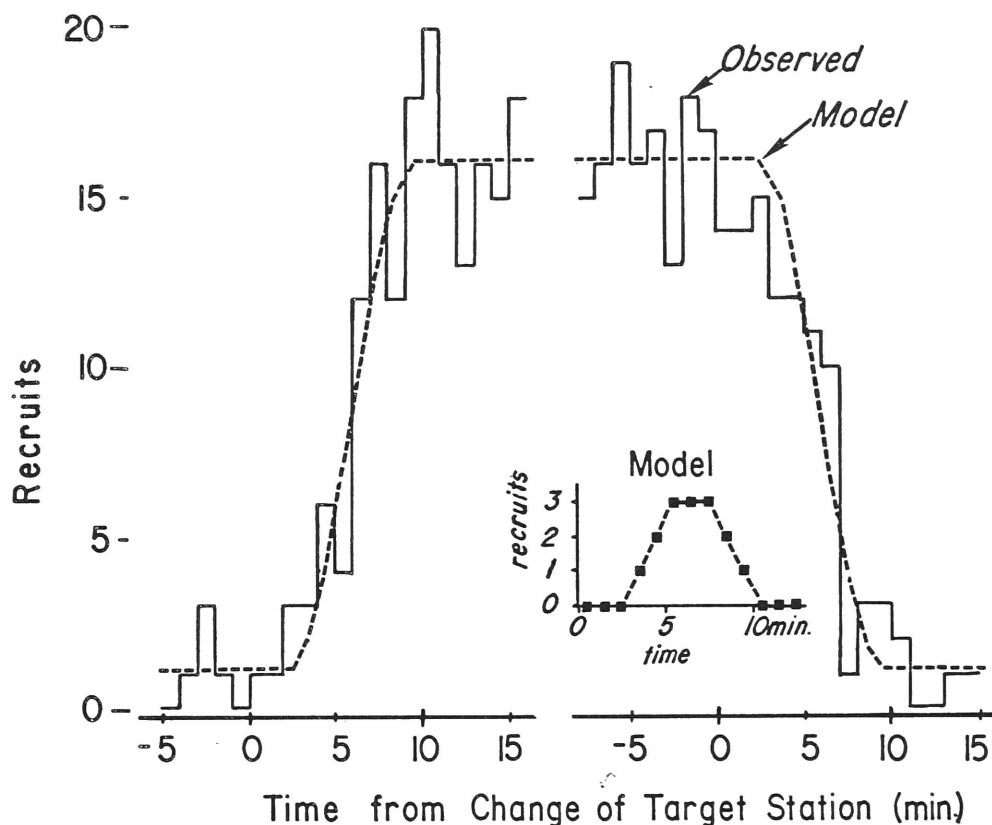


Fig. 64. Recruit Search Times. Left: the number of recruits arriving before and after a new station is signalled at 0min. Before the station is indicated by the dancing, a background level of recruitment can be observed. Recruitment reaches a maximum after about 10 minutes of dancing. Right: When the station is no longer signalled (at 0min) recruitment continues for a time, then falls off to a background level. These curves combine the results of experiments 1-6 and 13-14. Inset: a simple model of recruit search-time scatter such as the one illustrated can account for the results. In the model for this summed distribution, each minute of dancing is presumed to send out 15 successful recruits which arrive at the station over a period ranging from 3-9 minutes after the dance. (In the average single experiment, the rate would be less than one recruit per dance-minute.) Of course, the next minute's dancing would do the same, and so on. The various search-time curves would sum to create the dashed-line approximations shown in the left and right histograms.

available, whereas in the misdirection experiments there were usually 6 sites. An inaccurate bee might be more likely in this latter case to find a station -- albeit the wrong one -- on the first try. Since food sources in the field often exist in patches of considerable size, the misdirection results may be a more realistic measure of recruit search time under many conditions.

Although indirect, the analysis may be pushed still further. If the recruitment rate is relatively constant, and if recruits take various amounts of time to find the source (perhaps a function of the dance error), the scatter in recruit search times can, in principle, be inferred. The periods in which the recruit arrival rate increases, and in which it decreases after another station is signalled, are the significant times for such modelling. Unfortunately, the number of bees is so small (450) that the data are scattered. To increase the sample size it was necessary to include 4 distance experiments. In these cases there is a delay between the movement of the station to a new distance and the onset of dancing to that new distance. This delay -- about 1 minute -- was subtracted from the data from the distance experiments.

Nevertheless, trial-and-error fitting does yield a recruit search-time scatter which fits the data reasonably well. This model is shown in the inset in Figure 64, and the predictions it makes are indicated by the dashed lines in the left and right plots. The average delay of 6 minutes from dance to arrival at a station agrees reasonably well with the data of Gould et al. (1970), Esch and Bastian (1970), and Mautz (1971).

The recruit search times inferred from Figure 64 are still considerably longer than would be predicted on the basis of direct flight times. The delay from dance attendance to flying out of the hive is from 0-80 seconds (median of 35 seconds; Johnson and Wenner 1970). The direct flight time to the target is, depending on distance, from 20-55 seconds. These "overhead" delays total 1/2- 2 1/4 minutes. Hence, the average recruit required an additional 5 minutes to locate the food source. If the recruit flew to the location specified by the dance and then commenced its search, the rate of search might be inferred in a crude way. This further extrapolation of the data requires knowing how the bees are distributed in two dimensions -- a topic treated in the next section.

Theoretical Limits to the Accuracy of Recruitment

Direction accuracy must depend on how well the forager can measure the direction of the flight path, transpose that angle into the dance, and how well the recruits can measure and use that information.

Dance attenders might count or time the waggles, or count or time the sound bursts. Waggles may begin and end gradually, thereby introducing ambiguity into the measurements. Sound bursts, on the other hand, are likely to begin and end sharply. For the distances investigated in this work, each additional waggle corresponds to about 24 m (Fig. 5). How is it, then, that recruits in the misdirection experiments arrived more accurately than might be expected? Two possibilities come to mind: recruits might be counting the more frequent sound bursts -- a procedure with a resolution of about 10 m -- or, oddly enough, recruits might be exploiting the scatter in the dance. No two waggle runs seem the same either in distance or direction. If recruits attended, say, 6 cycles, they would have the opportunity to average the diverging signals. If, for example, a forager whose station were 200 m away attempted to signal the distance precisely, it would have to "choose" between performing 9 waggles (indicating 190 m) or 10 waggles (214 m). By performing some cycles with 9 waggles and some with 10 (4 and 2 of each, respectively, in this case), a signal accurate to within 2 m of the actual distance could be created. However, whether either the forager or the recruit could measure that accurately is doubtful. (By using the scatter in the more numerous and sharply-defined sound bursts, even higher accuracies would be theoretically possible.)

In reality, the dance scatter does not increase the accuracy of the indication nearly as much as is theoretically possible -- it could be 5-10 times more accurate than it is. Von Frisch and Jander (1957) measured the scatter in dance duration and were able to calculate that recruits would have to follow, average perfectly, and use flawlessly the information from a minimum of 5-6 waggle cycles to account for the accuracies observed in the step experiments. As von Frisch (1967a, p. 108) comments, "bees are not computers that work without making mistakes. Hence, since the assumptions stated certainly do not hold, more waggling runs must have been averaged..."

Nevertheless, bees really do only follow about six waggle runs (Esch and Bastian 1970; Mautz 1971; Johnson and Wenner 1970). One way out of this dilemma is to assume that recruits subsequently average different dances when they return to the hive after a fruitless search (as hypothesized by Lindauer 1971). However, the evidence that recruits return to the hive and attend new dances comes from experiments with only one food source (Esch and Bastian 1970; Mautz 1971), whereas the accuracy data comes from experiments with sizeable arrays (von Frisch 1967a, pp. 84-97 ; Gould 1974 and the experiments reported above). Since my data indicate that recruits do not take very long to find a food source (Fig. 64) when a large array is used, the idea that bees must average additional dances is not adequate. Since Lindauer's integration hypothesis depends upon the same phenomenon, the results summarized in Figure 62 also suggest that bees do not average separate dances.

Another way out of the dilemma that foragers can be sloppy while recruits must perform without error is to question the accuracy data itself. As experiments 9-12 indicate, von Frisch's technique of placing the Forager Station in the array exaggerates the apparent accuracy. Perhaps my accuracy data is more reliable, for although the experimental situation may not have been particularly "natural," at least all the stations were similar. Interpolating the values for 1 SD (standard deviation) in my direction experiments (i.e., 16.5% at 150 m, 8.5% at 400 m), the figure for 300 m is about 12.5%. For the forager dance alone, the SD is about 8.5% at 300 m (calculated from data in von Frisch and Jander 1957). Using the "sum of the squares" -- a method which accounts for the ability of two errors to cancel each other out -- the contribution of recruits to the scatter over and above that in the dance would be about 9.2%. Under my conditions, then, recruits and foragers perform with similar accuracies. There is a satisfying symmetry to this.

How Do Recruits Reach the Food?

Nothing is known about how recruits get from the dance in the hive to the food. Since no testable model exists, I offer the following one based on a small amount of observation and a great deal of analogy.

Recruits may be presumed to fly out from the hive at a typical flight altitude of 5-10 m (as indeed they can be observed to do) to the location interpreted from the dance. In doing this, they might fly over intermediate points with the proper odors -- as appeared to be the case in the distance experiments. Recruits may be supposed to arrive in the field and begin to search from a variety of positions scattered about the "target area" in a probabilistic fashion -- a function of the scatter in the dance and the recruits' error in interpreting and using that information. The searching strategy might be like that observed in wind tunnel studies of olfactory homers [Fig. 65]. Recruits arrive at low altitude from downwind. Their characteristic flight tone is quite distinct from that of foragers who maintain swift, high altitude flight until they are very near, finally swooping down quickly. According to this simple model, then, all of the downwind recruits would search crosswind until the odor plume is located, or until they give up. Once the odor is found, the recruit would follow it upwind to the source -- the station. They might search crosswind, in which case they would never find the food (Fig. 65, recruit #3), or they might drop downwind while searching across the wind (Fig. 65, recruit #4). On this point, the data, rather than being merely inadequate, simply does not exist. In the case of the strategy by which upwind-arriving recruits drop downwind, the recruits would find the stations downwind of their search point -- thereby reinforcing the distribution expected from the downwind-arriving recruits. Hence, the single best strategy for all recruits might be to cast crosswind while being displaced downwind until the odor is encountered.

Since recruits require a substantial amount of time to search in the field (about 4 minutes on the average based on my data), the distribution of searching recruits in the model described above can be used to produce a crude estimate of search time as a function of arrival distance downwind of the array. The simplest, least likely, but most convenient assumption for this calculation is that upwind-arriving recruits either do not find the array, or do so at the same rate as downwind-arriving recruits. It further simplifies the computation to assume, again without any empirical basis, that the search time is a linear function of the arrival distance --

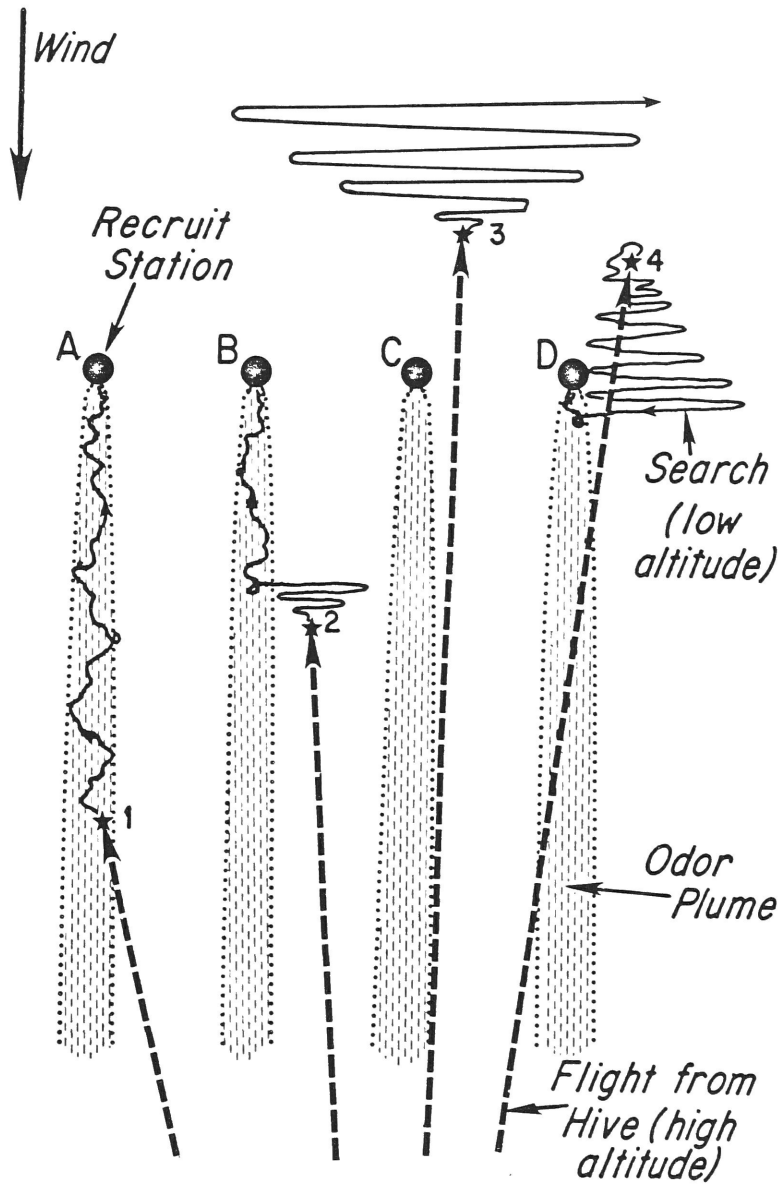


Fig. 65

Fig. 65. Recruit Search Strategy. This aerial view of hypothetical recruit strategies shows 4 Recruit Stations (A-D), each producing its own odor plume. (The odor emanating from a source is blown downwind, becoming broader due to diffusion and turbulence [Bossert and Wilson 1963]). No direct measurements of odor plume dimensions as a function of wind speed and turbulence have been made in the field, so these plumes are based on the wind tunnel plumes of Farkas and Shorey (1972). Recruits are presumed to fly out at normal flight altitudes -- well above the plumes -- to the location specified by the dancing (dashed lines represent the flight path; stars indicate the point of descent to search altitude). Recruits begin searching at low altitudes. Recruit #1 is pictured as descending directly into an odor plume, and then following it upwind in the manner described for moths (Farkas and Shorey 1972). Recruit #2 is pictured as descending into an area downwind without the food odor. This recruit is imagined then to begin casting about crosswind (as described for moths by Kennedy and Marsh 1974) until it enters an odor plume. The recruit then follows the plume upwind to the station. For purposes of illustration, the crosswind search is pictured with a slight movement upwind. In reality, it makes no difference whether the downwind-arriving recruit moves upwind or downwind. Recruits #3 and #4 are pictured as arriving upwind of the array. Recruit #3 is imagined simply to cast about crosswind, a strategy that does not result in encountering a plume. Recruit #4 is imagined as being displaced downwind as it moves from side to side across the wind -- a strategy which does result in finding an odor plume.

an equally unlikely possibility. The average search rate under these conditions would be about 10 m/minute -- a reasonably low figure based on observation of recruits approaching a station from as much as 10 m downwind. It goes without saying that recruit search paths need to be measured directly.

The Training Issue

The differences between the training techniques of von Frisch and Wenner appear to be crucial to the way by which recruitment is accomplished. The question arises of which situation (if either) is more "natural." This line of speculation requires knowing something about the ecology of honey bee food sources. For example, when a single, abundant, and (presumably) extensive crop is available, the odor of that source in the hive might grow strong enough to eliminate dance-language recruitment. Even in the early stages, however (just after the food is located), the dance language would be necessary to alert foragers to the new sources. The two training techniques, then, might be sampling two stages of the same process -- exploitation of an abundant food source. Von Frisch's experiments could be seen as examining the early phase, while Wenner's would be exploring the later phase.

Single, abundant, extensive food sources may be more typical of present agricultural practices than of the tropical forests in which the honey bee and its language evolved. In that case, the ability to direct recruits to a distant, isolated patch of food quickly -- either before it was found by another colony or another species, or before the potentially brief blooming period ended -- might have been a real advantage. A study of the foraging ecology of the three species of Apis still living in the forests of Asia, India, and the Philippines would be valuable. The distribution of colonies and food sources might be found to correlate with the distance to the "transition zone" between the round and waggle dance forms. Species such as Apis indica which have a very small round dance zone may have a very restricted foraging area and a high colony density, whereas Apis dorsata might represent the opposite situation. (Such a project should also look for races within these species differing in dance "dialect." The fact that these forest-living species are wont to be rather migratory should be borne in mind.) Since these tropical honey bees live on exposed combs, the odor of the food stores is not "trapped" in any cavity. This difference might be reflected in a much less noticeable tendency toward recruitment to odor alone.

THE DANCE-LANGUAGE CONTROVERSY IN RETROSPECT

Teleology and the Dance-Language Controversy

During the course of the dance-language controversy, the argument has been made both in print (Lindauer 1971; von Frisch 1974) and, more frequently, in private conversation, that since the dance correlations exist, they must have a purpose, and that purpose must be communication. This argument was made more systematically by Leibniz, although he invoked "God's will" instead of "natural selection" as the omnipotent agent. Voltaire's Candide illustrated the limitations of this point of view, but such parodies and gratuitous condemnations in our time have become the province of fundamentalist cranks. There can be no doubt that the assumption that "everything has a purpose" can be useful, but whether it has predictive value is another matter. It is not too difficult to imagine a selective advantage for something -- varieties of ungulate social systems, for example -- but often such speculation does not lead to the ability to predict anything -- leks for the Uganda kob, for instance.

The teleological argument rests on two assumptions: everything has an evolutionary purpose, and our guesses about those purposes are correct. Experience has shown that the null hypothesis -- that structures or behaviors are without a (known) purpose -- is not very fruitful. In the case of the honey bee, the elaborate dance manoeuver with its striking correlations provides a persuasive teleological argument for communication. In this example, the teleological hypothesis is based on the improbability of the dance correlations having occurred by chance, without evolution's having somehow acted to fashion a symbolic system of communication.

Upon closer examination, however, this argument seems to fail. The teleological hypothesis might predict that honey bees should outperform the many species of bees which lack a dance (and, hence, abstract communication). As Lindauer and Kerr (1958) showed, however, this prediction is incorrect. Stingless bees, along with many other social and non-social insects, display the ability to transform an angle flown (or walked) with respect to the sun (or any light) into an angle with respect to gravity. If this remarkable correlation must have a purpose, it cannot be

communication, since nearly all of these many insects obviously do not have a "language." If the correlation need not have a (known) purpose, then no purpose need be assigned uniquely to the honey bee. Similarly, striking duration-to-distance correlations have been observed in stingless bees (Esch 1967) as well as in other insects (Blest 1960). Here again, there is no evidence that information is being transferred to anything other than the human observer. If the distance correlations must have a purpose, then in the cases of the stingless bees and moths we must not yet know it. It follows that the "purpose" of the correlation in the honey bee dance might be the same, and hence both unknown and unconnected with communication.

To be consistent, the teleological hypothesis must assign a plausible purpose to the details of the dance. It must explain the purpose of the correlation between the distance of the food and the distance of the dance from the hive entrance (Boch 1956). It must explain the purpose of the scatter in the direction indications (particularly at closer distances). Since the degree of scatter correlates with distance, must its "purpose" be to indicate distance? Considerations of this sort quickly become absurd.

Logically, the teleological argument is not very useful as a method to deduce function conclusively. Its great value lies rather in its ability to suggest functions -- to provide testable hypotheses and hence to stimulate research. (As Tinbergen has said (1971, p. 323), no matter how convincing an observation appears to be, an experiment is required.) Used as a basis of proof or as an article of faith, however, it can merely reinforce our predispositions, stifling research by making further work seem unnecessary. Regrettably, the teleological argument is all too often put to the latter use.

Was the Controversy a "Revolution"?

The dance-language theory of honey bee communication is one of the most widely-known theories in animal behavior. According to von Frisch (1967a), forager bees return from the food and perform dances which contain relatively precise information about the distance, direction, quality, and odor of a source; and after receiving this information by attending dances, recruit bees "all" fly out "rapidly and with certainty" to the food,

displaying "incredible accuracy." Wenner and his colleagues began a long overdue challenge of that hypothesis, offering instead the theory that "all recruitment occurs by means of olfaction."

From the beginning, Wenner and his colleagues have cited the provocative Structure of Scientific Revolutions by T.S. Kuhn (1962). They see themselves as initiating a scientific revolution, bringing upon their heads all of the criticism and abuse supposedly predicted by Kuhn for such innovators. Although it was first designed to shed light on the Copernican, Newtonian, and Einsteinian revolutions, it is striking in how many respects Kuhn's description of a revolution fits the dance-language controversy.

According to Kuhn, "normal science" consists of elaborating, resolving, and expanding the dominant "paradigm." To Kuhn, a paradigm is more than just a theory; it is a conceptual framework within which scientists in a field design experiments, and interpret the results. Scientists involved in this usual sort of science are viewed as "puzzle solvers" ("run-of-the-mill scientists" according to Wenner) who know the expected result, but enjoy figuring out how to achieve that result in new and more precise ways.

Revolutions, according to Kuhn, come about when new paradigms replace old ones. The way in which the change of paradigms occurs is the focus of his analysis. "Discovery," says Kuhn, "commences with the awareness of anomaly...." Happily, even practitioners of normal science can have a role in this process, for "...novelty ordinarily emerges only for the man who, knowing with precision what he should expect, is able to recognize that something has gone wrong. Anomaly appears only against the background provided by the paradigm."

After allowing that there are always some anomalies, most or all of which may not represent real failures of the paradigm, Kuhn goes on to point out that some anomalies will clearly call into question explicit and fundamental generalizations of the paradigm. Defenders of a paradigm may respond to the discovery of anomalies by "devising numerous articulations and ad hoc modifications of their theory in order to eliminate any apparent conflict" with the data. Eventually, the persistent failure of the puzzles of normal science to come out as they should creates a genuine feeling of

insecurity in the field. Finally, an alternative hypothesis which offers a more satisfying explanation of the data may gain adherents and finally acceptance.

The new paradigm, Kuhn points out, may have problems of its own. Its acceptance depends on its ability to convince other scientists, and in this regard it is helpful if the new theory makes testable predictions not made or expected by the competing theory. During the period of competition, the debate will center on previously undiscussed questions of "legitimate" methods, problems, and standards of solution, although these will serve to define schools rather than to produce agreement. "The proponents of competing paradigms are always at least slightly at cross-purposes. Neither side will grant all the non-empirical assumptions that the other side needs in order to make its case." In short, "proponents of competing paradigms must fail to make complete contact with each other's view points," and even disagree about which problems any candidate for paradigm must resolve. Their standards of science, says Kuhn, are not the same.

Eventually the new paradigm may prevail through attrition: the adherents of the older theory simply die off. However it happens, the revolution ends with a return to normal science -- puzzle solving within the structure of a new paradigm.

When Kuhn's framework is applied to the honey bee controversy, a series of paradigms emerges. Aristotle provided the first paradigm for recruitment. According to him, recruits simply followed the forager to the food. The later observation that recruitment takes place even when the forager is not allowed to return to the food provided a fundamental anomaly. Von Frisch provided the second paradigm in 1923 when he proposed the hypothesis that bees locate the source on the basis of food odor in and on the bodies of dancing foragers. He also asserted that the round dance was used to signal nectar, whereas the waggle dance always meant pollen. This olfaction hypothesis worked remarkably well. In the 1940's, however, von Frisch noticed what he took to be another basic anomaly: recruits seemed to "know" the approximate location of the food before leaving the hive. Prompted to look more closely, von Frisch discovered the dance correlations and offered the dance-language hypothesis.

Each of these paradigm shifts may seem rather too bloodless and undramatic to deserve the description "scientific revolution." This is not to say that the dance-language theory was not received with considerable skepticism, but simply that because the main adherent of the old (olfaction) and new (language) paradigms happened to be the same person, the transition was facilitated. The dance-language hypothesis was so successful in gaining acceptance that it has never had to become very precise.

Wenner and his colleagues noticed what they believe to be fundamental anomalies in the dance-language hypothesis. First, they maintain that there are too many distance correlations in the dance. Although the redundancy does seem odd (the distance to the food correlates with the dance location, dance size, dance cycle duration, waggle cycle duration, number of waggles per cycle, number of sound bursts per cycle, duration of sound bursting per cycle, etc.), the anomaly Wenner (1971) chooses to emphasize is irrelevant: "The dance-language hypothesis as originally formulated and as generally accepted did not include the prediction that dancing bees would produce sounds."

The second anomaly is that von Frisch's bees performed too well in the step and fan experiments. Von Frisch realized this problem, and made an ad hoc modification of the hypothesis which allowed bees to average successive dances. The scatter in the dance is so great that von Frisch had to observe more than two hours of successive dances before he felt confident to set out to find a forager station his students had hidden (von Frisch 1967a, pp. 227-230; a less precise measurement can be obtained in perhaps a minute, but even so, recruits attend dances for only 6-15 seconds). As discussed above, my data indicate that recruits presented with an array do not average separate dances, and that the accuracy of bees in von Frisch's arrays is, as Wenner maintains, partially a result of putting the forager station in the array.

The third anomaly in the dance-language paradigm is that recruitment can occur without dancing, and in fact does so regularly under Wenner's conditions. Von Frisch was, of course, aware of this phenomenon, but failed to emphasize it strongly. Wenner is probably right to assign danceless recruitment the major role under most conditions (see Free 1969), but

even a rare phenomenon can still be real and significant. Although Wells and Wenner (1973) call it a sign of bias, the statement of Gould, et al. (1970) is nevertheless true: "Simply demonstrating that olfactory cues are sufficient in a particular situation does not mean that the dance language is not used under other conditions." Wenner (1971), however, holds to the widespread attitude that an animal is a simple system, and can only behave in the single simplest way. He argues that "one cannot have it both ways. A recruitment by dancing cannot be both necessary and not necessary in the same circumstance." The implications of this attitude will be explored below.

The fourth anomaly Wenner finds is that without odor at a food site, recruits cannot find it. Opinions on whether this observation is true differ. Gould, et al. (1970), for example, obtained excellent recruitment with unscented solutions. It is unclear why this should be considered an anomaly in any case. Von Frisch's hypothesis does require recruits to use odor information once they reach the general area of the goal. If the goal is odorless, even the most accurately guided recruits might experience difficulty.

Wenner also finds that recruits take too long to find the food. Clearly, this is a matter of degree. The enthusiastic statements of von Frisch and his colleagues -- "rapidly and with certainty," for example -- do not agree with the data. Why recruits take so long is not known.

The sixth anomaly is that there is no correlation between dance vigor and the sucrose concentration of the food. Although von Frisch observed such a correlation, he warned that "it is not to be defined quantitatively." Wenner, et al. (1967) were able to confirm that prediction, concluding, however, that no correlation exists. Since virtually all researchers agree that the dances really are more vigorous when the sucrose concentration is raised, it is odd that, as yet, no measured parameter has been correlated. The most likely candidate at this point might be waggle extent. The number of cycles performed correlates with increasing food quality to a point, but at higher sucrose concentrations foragers perform fewer, albeit more vigorous, dances (almost as if they were "in a hurry" to return to the food).

The seventh anomaly is that not all of the recruits find the food source.

The eighth and final anomaly is, oddly enough, that bees learn. According to Wenner (1971), "virtually everyone working with bees has begun his investigation with the assumption (implied or stated) that learning is not involved in bee recruitment." Since learning of odors, shapes, locations, compass directions, and times have been demonstrated in honey bees for 20-60 years (reviewed by Wells 1973), and are all necessary and obvious even in the process of training foragers, it is difficult to know what Wenner might have in mind by this remark.

In any case, these anomalies led Wenner to wonder whether the olfaction hypothesis might not explain all the data. Upon closer inspection, he found that none of von Frisch's experiments were sufficiently well controlled to exclude the intuitively simpler odor explanation. In several experiments, odor alone did seem to explain recruitment. When Wenner and his colleagues encountered the natural conservatism and skepticism of fellow scientists, they were reminded of Kuhn's observation that scientists are slow to embrace a new paradigm. In practice, Kuhn says, this patience with a major anomaly may prove justified. Just as Kuhn predicted, the controversy often focussed on methodology and standards of proof, with a great deal of talking at cross purposes.

Wenner felt that many scientists were "very annoyed" at his criticisms of von Frisch in an emotional way that only defensiveness could engender. The tone of Dawkins (1969) suggests that in some cases he may be correct: "Wenner and his colleagues presume to challenge the findings of a great scientist" (my emphasis).

In some cases, there has been a failure to tolerate not so much a new view as the uncertainty -- the "essential tension implicit in scientific research" (Kuhn 1962). As Wenner puts it, "the desire for certainty overrides our doubts." The ability to tolerate doubt -- while at the same time avoiding apathy or the conviction that the thing cannot be known -- is an often neglected characteristic of the good scientist, and perhaps of the inquiring mind in general. Ironically, the Romantic poet Keats (1817) made the most acute definition of the scientific mind when he attempted to define

the humanistic seer: "It struck me what quality went to form a Man of Achievement, especially in Literature, & which Shakespeare possessed so enormously -- I mean Negative Capability, that is when man is capable of being in uncertainties, Mysteries, doubts, without any irritable reaching after fact & reason."

Another quality of a good scientist may also deserve more emphasis -- the ability to imagine the unthinkable. As Griffin (1975) points out, the application of Morgan's Canon and other such "simplicity filters" has overcorrected an earlier tendency to anthropomorphize animals. Too much skepticism may become a blinding bias against yet-undiscovered sensory modalities and processes in animals. Another Romantic formulation, Coleridge's concept of a "willing suspension of disbelief" (1817), may often be as useful an attitude as a hard-nosed skepticism.

Throughout the dance-language controversy, Wenner has made perceptive and valuable contributions. Von Frisch's controls do not exclude the possibility of olfactory recruitment alone, and Wenner is certainly correct in saying that an endless repetition of ambiguous experiments does not add anything to the evidence. He is also correct in asserting that all of the previous evidence for the existence of a dance language was circumstantial. Wenner is probably right in refusing to be persuaded by teleological arguments, even when the catchword "evolution" is added. He has reminded us of the great importance of olfactory recruitment in honey bees, and by that, affected the scope and course of future research.

But, in the end, the dance-language paradigm cannot be discarded. However imprecise it has been allowed to remain, however much its emphasis has exaggerated the "exotic" aspects of honey bee communication, the misdirection experiments provide evidence that admits of no other explanation than that von Frisch is correct, and that honey bees do have an abstract system of dance communication. Perhaps the time has come for "normal science" to face the less interesting situation, not sketched for us by Kuhn, of dealing with the aftermath not of a revolution, but of a scientific "uprising" which has served the valuable purpose of forcing upholders of the dance-language paradigm to provide objective evidence in its defense. Perhaps it is time for "normal science" to work out the details -- the

absence of which Wenner has so forcefully noted -- of this remarkable system of communication and recruitment.

The Dance-Language Hypothesis: A Reformulation

In order to be a useful theory, able to make testable predictions, the dance-language hypothesis must be restated in terms as precise as possible. Regrettably, such an attempt cannot proceed very far without more data. Excluding swarm dances, we may begin by saying that foragers collecting from nectar, pollen, propolis, or water sources return to the hive and, under some circumstances, may dance. The readiness to dance depends in some qualitative way upon the needs of the hive. Dancing is most common when the item being advertised is in very short supply. The speed with which hive bees relieve foragers of their loads also affects the readiness to dance. The relative quality of the source is reflected by the vigor of the dance. The "goodness" of a food source is related in at least a qualitative way to the sugar content (von Frisch 1967a, pp. 236-238; sugars vary in their ability to release dancing), viscosity (von Frisch 1967a, p. 239), odor (Kashev 1957; higher scent levels inhibit dancing), distance (Boch 1956; sources farther away must be sweeter), the quality of competing sources (von Frisch 1967a, pp. 246-253), the form of the food container (Kappel 1953), and so on. Despite these qualitative correlations, researchers are unable to make feeding stations more attractive than natural food sources (von Frisch 1967a, p. 18). Clearly, something else which is important is still to be discovered.

A newer dance-language hypothesis might continue by stating that the dance indicates the approximate distance to the food source in some way associated with the waggle phase of the dance. The misdirection experiments reported above strengthen the case for distance communication. Although at present it may be possible to tentatively exclude some of the distance correlations as too inexact to explain recruit accuracy, there is no way from present data to isolate the salient features of the dance.

The approximate direction to the food source is indicated by means of the dance orientation. The misdirection experiments varied this component independently, providing good evidence that the dance orientation is the most important direction cue.

The scatter of the distance indications is large, but the SD for six successive waggle runs is approximately constant to 1 km, and slightly larger at greater distances. Of course, why there is any scatter at all, and how foragers measure the distances is not known. The exact magnitude of the scatter cannot be calculated until the crucial cues in the dance are known.

The scatter of direction indications is very large at short distances, but small at greater distances. Why the scatter should vary with distance is not known. It could serve to specify a constant "patch size."

Potential recruits attend dances for about six cycles. Through unknown sensory channels, the distance and direction correlations are detected, and are then processed and averaged in some way. Presumably a recruit's "gravity detectors" inform it of its own orientation. How the orientation of the dance is determined is not known. Since the important distance signals are not known, the sensory channels cannot yet be inferred with certainty.

The odors on the forager's body reflect the odors at the food source. The dancer sometimes offers food samples which may provide recruits with additional information about the quality and odors of the source. Since the vigor of the dance may be altered without changing the concentration of the food merely by using different feeding station designs, the possibility that the food samples provide quality information may be tested. Von Frisch (1923) concluded that odors carried internally by the dancer in the food were important, but he did not completely exclude the possibility that in grooming themselves, foragers applied the food odor to the outsides of their bodies where it could be detected by recruits.

Some recruits leave the hive, and some smaller number find the food. If an array is used, most recruits locate the food on the first trip. If only one station is set out, or if low levels of odor are used, recruits may return to the hive and attend additional dances. The average successful recruit requires far more time to locate a food source than would be expected if it flew directly there. The numbers associated with this section of the hypothesis vary widely. The reasons for this variance are not known. The way in which recruits get from the hive to the food is not understood.

In locating a food source, the odors of the hive and the scent gland as well as of the locale and food may be important. The appearance of the source and the presence of bee-sized objects help to induce recruits to land.

Although recruits arriving in the field show a preference for the approximate distance and direction indicated by the dance, there is considerable scatter. The error displayed by recruits is in excess of the error contained in the six or so dance cycles which they observe. To what extent this recruit scatter arises from errors in interpreting the dance, residual misdirection, problems of memory, or errors in using the dance information in the field is not known.

The dance-language hypothesis is only a partial description of recruitment. The mechanisms underlying this remarkable communication system are even less well understood. Clearly, there is a great deal to be learned. Hopefully, this reformulation emphasizes the questions as well as the partial answers.

THE DANCE LANGUAGE AS A "LANGUAGE"

The Information Content of the Dance

The dance may be considered as a sentence which states the distance and direction of a food source, as well as its type, quality, and odor. The message is "noisy," but then it is generally repeated several times. By their behavior, recruits indicate what sorts of information they have received, and provide a convenient and conservative estimate of the amount and quality of that information. Information theory (Shannon and Weaver 1949) maintains that information can be measured, and that something is to be gained by measuring it. More recently, information theory has been applied to animal communication (e.g., Haldane and Spurway 1954; Wilson 1962, 1971; Altmann 1965; Hazlett and Bossert 1965; Dingle 1969). In principle at least, the information content of the honey bee dance can be measured and compared with that of other species. In fact, however, certain practical difficulties arise in the attempt.

Information theory measures the information in a signal in terms of the amount of uncertainty which the message abolishes. The uncertainty, then, must depend upon the probability of receiving that particular message. (Judging the probabilities in an animal communication system is often very difficult.) Shannon and Weaver (1949) choose to measure information in "bits." In the simplest case where all signals are equally probable, the number of bits (H) is given by:

$$H(x) = -\log_2 p(x)$$

where $p(x)$ is the probability of any particular signal. In this case, then, one bit is the amount of information necessary to distinguish between two equally probable signals. For cases in which the signals are not equally probable, the information is given by:

$$H(x) = -\sum_{i=1}^r p(i) \log_2 p(i).$$

Both of these functions apply to discrete (digital) signals. In the case of graded signals, however, where the (analog) value being signalled varies about an average in a statistical fashion (as in the distance and direction indications of the dance), the number of bits is given by:

$$H(x) = \frac{\log \frac{r}{SD}}{\log 2} - 2.047$$

where r is the range of values (0-360°, for instance) and SD is the standard deviation (Haldane and Spurway 1949). This formula assumes that all values within r are equally probable.

The amount of information in a dance depends upon the uncertainty which the signal abolishes. If only one food source exists, and it has been actively exploited for some time, then another dance specifying that source contains little or no information. Haldane and Spurway (1954) and Wilson (1962) calculated the information content as though all alternative locations were equally probable, implying an infinite number of sources. Their values, then, actually represent a kind of repertoire size rather than

a measure of information in the sense of Shannon and Weaver (1949). As Wilson (1971) points out, the von Frisch data are inadequate even for this calculation, and "only new data can establish the true value with any confidence." I propose to calculate in a very inexact way both the repertoire size and the information content of a hypothetical dance. In the hypothetical case, four different food sources will be presumed to be offering both pollen and nectar and to be distributed more or less evenly about the hive at distances up to 2 km. The reasons for the inexactness of the calculation will quickly become apparent.

Computing the information transmitted by the dance's direction signal depends upon knowing the SD. Unfortunately (and unaccountably), the direction scatter depends upon distance, being very large at closer distances, but becoming very small at longer distances. The SD's from my measurements and those of others are 16° at 150 m, 5° at 400 m, 4° at 750 m, and 3° beyond 1 km. Taking 4° as an average value, the direction component of the dance (as judged by recruit behavior) transmits 9.3 bits of information.

Computing the information transmitted in the dance distance signal depends upon knowing both the SD and the distribution of dances to various distances. Happily, the SD is nearly constant: 38 m at 150 m, 45 m at 315 m, and 60 m beyond 1 km. Taking the value to be 50 m in the hypothetical case, the information transmitted in the dance would be 3.2 bits if all distances had an equal probability of being signalled. In fact, however, closer sources are preferentially indicated. To calculate the repertoire size, the range of distances which may be signalled must be determined. In theory, the dances could be performed to indicate any distance (e.g., a dance cycle indicating 100 km might last six minutes), but physiological considerations such as flight range must set practical limits. The longest distance to which bees have yet been trained is 12 1/2 km (von Frisch 1967a, p. 73). Taking 12 km as the range, and using a SD of 60 m, the repertoire size of the distance component of the dance is 5.6 bits.

The dance also contains information about the odor of the food. In the hypothetical case, four different species of plants were supposed to be offering nectar and pollen. In this case, the food odor would provide 2

bits of information. In terms of repertoire size, the appropriate number to use is in doubt. As a lower estimate, the test by von Frisch (1923) may be used. He demonstrated that bees could distinguish 46 different floral odors -- about 5.6 bits of information. On another occasion, recruit bees located the correct type of flower in a garden containing 700 blooming species -- 9.6 bits of information. As an arbitrary (and hopefully conservative) estimate, I will suppose that recruits can distinguish 100 odors -- 6.5 bits of information.

In addition to the odor of the food, the dance contains information about the odor of the locale. No quantitative tests of recruit acuity have been performed, however. Since locale odors may be redundant with the distance and direction correlates, this class of information will be ignored.

The dance also specifies the type of food. In the hypothetical case, the food is either nectar or pollen -- 1 bit of information. The repertoire, however, also includes propolis, nest cavities, and water (although water may be considered as merely very dilute nectar, and hence not really a distinct food type) -- 2 bits of information.

The dance also contains a "vigor" element specifying the quality of the food source. At present there is no data on how many levels of vigor recruits are able to distinguish. As a hopefully conservative estimate, 4 levels will be assumed -- 2 bits of information.

On the basis of these calculations and guesses, then, the hypothetical dance may be said to contain 17.3 bits of information. This value corresponds to 135,000 discrete "sentences." The repertoire size of the dance language may be conservatively estimated to be 25.4 bits -- 40,000,000 discrete sentences.

These are large numbers, and need to be put into proper perspective. Altmann (1965) found the information content of the average signal of Rhesus monkeys to be 5.3 bits, a far cry from the honey bee's 17.3. The repertoire size of the chimpanzee Washoe (Gardner and Gardner 1969) is larger. Washoe ultimately learned about 130 discrete signs. To avoid underestimating the potential repertoire size, we may assume that Washoe

might eventually be able to use all of her signs in four-word sentences of the form noun-verb-modifier-noun. Assuming that Washoe knows about 70 nouns, 30 verbs, and 30 modifiers, the potential repertoire size would be about 21.7 bits -- 3,250,000 discrete sentences. Of course, only a fraction of the theoretically possible sentences would make sense. Nevertheless at 40,000,000 sentences, the honey bee repertoire is clearly larger. Whether the current attempts to teach chimpanzees will reverse this picture remains to be seen (Rumbaugh, et al. 1973).

The repertoire of human speech, on the other hand, does seem to be significantly larger. A precise estimation of the information content of the English language is probably not possible, but it may be reasonable to set some approximate lower limit. Although English dictionaries may contain 450,000 words, a "typical" person may use only 10,000 of these. Although sentences may be of nearly any length, a typical pattern might be auxiliary-adjective-noun-adverb-verb-adjective-noun. We may arbitrarily assume that this hypothetical vocabulary contains 6500 nouns, 1500 adjectives, 1000 verbs, 500 adverbs, and 500 auxiliary words. If we make the conservative assumptions that all signals are contained in single sentences of this sort, and that intonation and gestures add no information, then the information content of a single sentence would be 74.3 bits -- about 24,000,000,000,000,000,000,000 (2.4 x 10²²) discrete sentences. Of course, many of the theoretically possible sentences would be nonsense, while others might be redundant. Although honey bee communication can transmit vastly more information than virtually any other known animal system, it looks small indeed when compared with even a minimum English language. Whether the information content of a communication system is relevant, and whether comparisons between distantly related species are valid are different questions.

Do Honey Bees Have a Language?

Definitions of language often seem more expressions of personal taste than exercises in putting particular, intuitively obvious phenomena into concise, concrete formulations. Too often, definitions of "language" are merely transparent attempts to exclude all examples of non-human

communication. Recent years have witnessed an evolution of such definitions. The strategy, according to Fouts (1973), being that "when evidence is presented that a non-human species achieves some of [the previously proposed criteria for distinguishing human language], the list grows longer to exclude the interloper species. If this kind of progression continues, we may eventually have a definition of language which isomorphically maps the behavior of human beings." (Such a "map" may already exist in the 16 "design features" of human language formulated by Hockett and Altmann [1968].)

Thomas Pyles (1971), author of a standard text in linguistics, defines language as "systematized combinations of sound which have meaning for all persons in a cultural community." Although he successfully excludes by this definition the "fetching" chimpanzees which have been taught both a vocabulary and grammar, Pyles is left in the awkward position of having to explain why American Sign Language and written English do not constitute "real" languages. Ronald W. Langacker (1973) is more cautious, allowing that "the acquisition of language is...in no way dependent on verbalization." Langacker defines language as merely a "set of principles establishing correlations between meanings and sound sequences," and is careful always to modify the word "language" with the adjective "human." Although Langacker considers human language to be unique, he allows that in many ways it differs from animal communication only in degree.

For Pyles, on the other hand, language is an "exclusively human phenomenon," differing from animal communication in kind rather than merely in degree. This attitude implies that there is no evolutionary continuum between animal communication and human language; and, hence, there is nothing relevant to be learned by studying systems of animal communication. As Pyles puts it, "it is language that makes our species human, strikingly differentiating us from all other species." Mortimer J. Adler (1967), too, concludes that the essential difference between humans and animals "rests only on the pivotal fact of human language." The examples of this opinion are virtually endless (admirably reviewed by Griffin 1975), and all reflect the attitude that only humans could have language. Yet neither the definition of Langacker nor the one by Pyles, in themselves, exclude animal communication. Clearly, for them "language" must have other necessary features.

Although Adler never formally defines language, he is able to list his criteria concisely. Adler states that 1) animals cannot ask questions ("none except man can ask for...a banana") or use parts of speech; 2) animals do not learn or intentionally use signs; 3) animals (and primates in particular) do not make human speech sounds even though they possess the vocal apparatus to do so; 4) animals do not and cannot be taught to initiate cues to elicit behavioral responses in humans or other animals; and 5) animals do not possess the complicated brain and hemispheric dominance which is necessary for language. In reality, none of Adler's criteria constitute fundamental distinctions. Item 5, the physical size and nature of the brain, is completely hypothetical (humans do not have the largest brains), and contrary to Nottebohm's (1971) finding of hemispheric dominance in song birds. Item 4, initiating cues to affect the behavior of others, ignores fifty years of work with operant conditioning, the whole of contemporary ethology, and the everyday experiences of owners of dogs and cats. Item 3, the vocal apparatus, is simply wrong (Lieberman [1968] and Lieberman, et al. [1969] have demonstrated that primates lack a pharyngeal region whose cross-sectional area can be altered, and hence cannot produce the variety of vowel sounds necessary for human speech; why they should experience difficulty in producing the much narrower range of sounds which are theoretically available to them is unclear). Items 1 and 2 (asking questions and using signs), as well as item 4, are each contradicted by the recent work of Gardner and Gardner (1969), Premack (1971), Ploog and Melnechuk (1971), Rumbaugh, et al. (1973), and Fouts (1973, 1974). In each case, a chimpanzee was taught to ask questions, express opinions, and control the behavior of humans (and, perhaps, even of conspecifics).

To be fair, Adler's criteria were drawn up before Sarah, Washoe, and Lana began teaching us about the abilities of primates. The distinctions which Pyles and Langacker make, on the other hand, were made with the benefit of reports of the chimpanzee work (they generally cite Time magazine). Pyles escapes the problem through the irrelevant requirement that language be verbal. Gratuitously, however, he adds that human language is unique in that it is "open" (meaning that new symbols may be

added), "making possible the production of an infinite number of different sentences." (Whether an infinite number of sensible and non-redundant sentences is possible is another question.) As a result, says Pyles, only man is able to talk about his subjective experiences.

Langacker, too, points out that only human language possesses an "unlimited set of discrete signals." Langacker states that "if the difference between human language and natural animal communication systems had to be summarized in one word, a good choice for that word would be novelty." Implicit in virtually every formulation of the concept "language" is the belief that "real" or "true" language requires the user to be a rational creature who learns his communication system and is able to create new signs and combinations of signs according to the system's arbitrary rules of grammar; and who, having free will, is able also to break or change those rules. This concept of language may ultimately survive the chimpanzee experiments and successfully exclude all other animals. Still, the observation that primates can discover, learn, and pass on new behaviors (Tateishi 1958; Miyadi 1959), combined with the work of Rumbaugh, et al. (1973; Rensberger 1974a,b) in which Lana displays an acute sensitivity to and irritation with non-grammatical sentences, suggests that even this very exclusive definition may not "work." As it stands, the definition may well be too restrictive. It may exclude various hypothetical communication systems which would still satisfy our intuitive sense of the concept "language."

Imagine that a tribe of obviously rational beings were to be discovered which possessed a communication system remarkably similar to, say, English, except that the beings were unable to invent new signs. Suppose that these imaginary beings could use or combine signs in completely new ways, but some limitation simply prevented them from adding new signs (for example, suppose the signs were gestural, but all physically possible gestures were already defined). Could these rational creatures be said not to have a language? Perhaps the ability to create new symbols is not crucial. Or again, suppose that these creatures, still rational and fully aware of what they are doing, were born already knowing their system of communication (but were still able to invent new combinations of signs, ask questions, express doubt, and so on). (The increasing

evidence that human grammar and consonants are instinctive [e.g., Langacker 1973, pp. 239-259; Eimas, et al. 1971] adds a certain relevance to this example.) Again, could these beings be said not to have a language?

An important objection to this line of argument might be based on Adler's opinion that rationality and language are equivalent. As a result, my hypothetical beings could not be both rational and yet unable to fulfill the rest of the criteria for possessing a language. Perhaps the concept most in need of a definition is not "language" but "rationality."

Are Honey Bees "Rational"?

In seeking to discover whether the study of animal communication in general, and the honey bee dance language in particular, is relevant to understanding human language, we have had to infer an intuitive definition of "language." It seems clear that honey bees have a language in the simple and explicit sense of both Pyles -- "a systematized combination of [symbols] which have meaning for all [individuals] in a given cultural community" -- and Langacker -- "a set of principles establishing correlations between meanings and sequences [of symbols]." When the implicit criterion of "rationality" is added, however, it is no longer clear whether honey bees may be said to possess language.

The question becomes whether honey bees are rational -- do they "know what they are doing"? In order to answer the question, we must first decide what is meant by the term "rationality." Happily, Jonathan Bennett's (1964) charming book Rationality considers this problem in detail, using the honey bee as the primary example. Bennett sets out to prove that honey bees are not rational creatures. Because there are several difficulties with his arguments, a closer look at his conclusion that bees are irrational may be justified.

In contrast to others, Bennett begins his analysis by explicitly divorcing language from rationality. His rather sensible criteria for language includes rules (grammar), "words" which are symbolic, complexity (in the sense of many possible sentences), and behavioral evidence of communication. The honey bee dance language appears to satisfy each of

these explicit criteria. But, says Bennett, language alone does not imply rationality. Even though animals using a language may be guided by rules, to be rational they must be aware of those rules. This element of self-awareness may be the implicit criterion missing from the explicit definitions of linguists wishing to exclude systems of animal communication. The question immediately arises, however, of just how we are to know if an animal is "self-aware." As humans, we conclude that we are rational through introspection. We conclude that other human beings are rational -- self-aware -- first through observation, and then through analogy with our own behavior. For a phylogenetically distant species such as honey bees, however, all of the dangers of anthropomorphizing arise. As a result, Bennett observes, objective criteria are needed.

Bennett begins formulating his list by stating that the mere number of sentences in a language is irrelevant. He must do this, since he believes the number of honey bee sentences to be infinite. As was demonstrated above, information theory can be used to set a finite limit on the number of meaningfully discrete sentences in the dance language (and perhaps, if we knew how to calculate it, in human language as well).

Bennett's strategy is first to show that honey bees cannot do something that we might intuitively expect a rational creature to be able to do, then to create an imaginary bee which can do it, and then show that the requirements of rationality are still not met. In the end, we are persuaded not only by the hypothetical honey bee's inability to meet the final criterion, but also by the long list of former criteria not met by real bees. Several of the items on this list, however, either do not belong there, or are criteria which honey bees do seem to satisfy.

Bennett states that honey bees cannot be rational since they do not realize when the rules of the language have been broken. As a result, they have no linguistic or behavioral expression for "not true" or "I doubt that." Of course, behavior is the only sort of evidence available to us. One effective way of denying the truth of a statement might be simply to ignore it. Since many dance attenders do not leave the hive, their behavior could be interpreted as expressive of doubt. Another effective form of denial might simply be a counter-assertion: dancing to indicate a

different station. More significantly, attenders never leave the hive after rule-breaking "silent" dances (Esch 1967), and even attack dancers which break the rule that food samples must be offered after a stop signal (Esch 1964). This evidence suggests that bees can indeed detect when rules are broken.

The sort of behavior Bennett offers as constituting a satisfactory and convincing example (if it existed) of a honey bee's ability to express doubt would require recruits to learn that a particular dancer is unreliable, and so attack or ignore it. As with many of Bennett's examples, the 60,000-100,000 bees in a hive would be required to recognize each other individually. Perhaps individual recognition is, in the end, Bennett's basic implicit criterion. Although there is no evidence for individual recognition (though foreigners -- bees from other hives -- are recognized), it is entirely possible that recruits could learn to associate the odor of a particular source with an aversive stimulus, and hence come to at least ignore dances advertising such a source. It is an experiment which may never have been tried.

Bennett goes on to state that honey bee behavior is typical of a non-rational stimulus-response system, and as such does not involve the rational faculty of "judgment." But in fact, honey bees do seem to make comparisons and decisions. Recruits may attend dances specifying several different sources before flying out to a particular food site. Foragers regularly collecting food from a source sometimes encounter dances by other foragers. On occasion, if the dances indicate significantly better food, foragers may switch to the competing source. A more dramatic case is observed during swarming when the locations of several potential nest sites are being signalled simultaneously. In such cases, recruits have been observed (Lindauer 1955) to follow dances to one site, visit that site, follow dances to another site, visit that site, and then begin to perform dances to one of the two. In all three cases, comparisons seem to be made and acted upon.

Bennett maintains that the presumed stimulus-response nature of honey bee behavior which precludes rationality is further demonstrated by the inability of bees to learn by trial-and-error. Again, honey bees are

more subtle than Bennett believes. In fact, there are so many examples of trial-and-error learning that it is difficult to know which one to choose as an example. A classic instance involves the honey bees' interactions with alfalfa blossoms. Alfalfa flowers possess a "spring-loaded" anther which is tripped by entering bees. The size of the bee determines the way in which the anther strikes the insect. A large bumble bee, for example, receives a minor tap which deposits pollen on its back. (The pollen is carried to the next flower, thereby effecting outcrossing. Alfalfa seems to have coevolved with the bumble bee.) The smaller honey bee, on the other hand, receives a violent blow, and may even be thrown out of the blossom. Most honey bees learn to avoid alfalfa after a single encounter (Lovell 1963). Other honey bees, however, learn one of a number of strategies for avoiding the anther (Reinhardt 1952; Pankiw 1967). Some bees learn to distinguish between tripped and untripped flowers, entering and collecting only from those which have been tripped, and are therefore "safe." Other bees learn to "rob" the blossom by removing the nectar without entering the flower (chewing a hole in the side is one strategy). None of these examples appear to be cases of rigid, stereotyped behavior.

Bennett proposes and then discards another criterion: rational creatures must have a language with a future tense. The problem here is that if Bennett is not careful, he could exclude certain human languages. Instead, the criterion is modified to require the bees to recognize signs that food will be at a location in the future. As in so many instances, the problem arises of how we are to know whether or not bees can deal in these terms. When foragers learn that a particular source is available at a particular time of day, and begin to arrive and hover about the location just prior to the appropriate time (von Frisch 1967a, pp. 253-255), may we not infer that they "know" that food is likely to appear soon? When foragers learn to associate the presence of a particular investigator with food, and hover around and follow that person for considerable distances until the food is produced (von Frisch 1967a, p. 23; Gould, unpublished), may the bees not be said to anticipate the experimenter's typical behavior? When foragers learn that a food source is being moved systematically either toward or away from the hive, and so anticipate the movement, hovering at the next location (von Frisch 1967a, p. 17), may not the bees

be said to be making a prediction about the future? Observations of this sort suggest that Bennett may not be correct in concluding that bees have no concept of the future.

Bennett goes on to argue that the irrationality of bees is also demonstrated by the failure of recruits to perform dances without first having visited a food source, even though they possess the abstract information to do so after attending a dance. Presumably the logic here is that dancing is part of a rigid stimulus-response chain such that dancing may only occur after flight. Of course, recruits often visit a source without dancing upon their return. If recruits really were to attend dances and then perform imitations of the dances before flying out, those who prefer to view behavior according to a stimulus-response paradigm would merely rearrange the presumed chain. This criterion is therefore not useful, since any alternative behavior could be explained in the same way.

Bennett argues that bees cannot be rational because they cannot "lie." Of course, treated foragers in the misdirection experiments were caused to lie, but not in the conscious sense Bennett has in mind. As a colony of closely related individuals, however, honey bee workers have nothing to gain by misdirecting other members of the hive. A rational animal, we may suppose, ought to lie only for a reason. Perhaps bees lack good reasons. (How lying bees could even be observed is another question.) This criterion, then, may not be useful in the present circumstances.

The last two criteria which Bennett proposes are more substantial, and seem to strike at the core of the issues of both language and rationality. The first is that a rational animal should be able to combine old symbols in a new way, or be able to invent new ones, to handle new situations. This raises again the example of the hypothetical beings with a communication system meeting all criteria but this one. Whether this sort of "creativity" is crucial to either language or rationality is, in the end, probably a matter of individual preference.

Bees may, in fact, have little or no ability to create new signs or sign combinations. The case of dances to nest cavities may not be taken

as an example of inventing a new use for old symbols since bees all seem to indicate nest cavities in the same way. If bees were able to use new symbols or new combinations of symbols to describe new situations, some variability in the exact choice of symbols would be expected. (Just what the variability or "scatter" in the dance correlations may mean in this context is another question.) Whenever bees have been presented with what must be very rare situations, they have solved the problems in a single (albeit often unexpected) way. For example, when a hive was placed at the top of a sheer vertical cliff and foragers were trained to a food source 53 m below, the dances indicated a direction directly away from the cliff (von Frisch 1967a, pp. 165-167; no variation in dances was reported; regrettably the distance signalled by the dancing was not recorded). In the complementary experiment, the hive was located at the bottom of the cliff, while the feeding station was suspended from a pole 53 m overhead. In this case, the dances indicated the direction directly into the cliff. (Again, the distance signalled was not reported. The experiment of extending the pole until the station would actually be in the direction away from the cliff relative to the hive was not tried.) In both cases, recruits successfully located the food.

The distance signalled in the dance is thought to be judged on the basis of "effort" (e.g., a walking forager bee signals 20 m after only walking 2.5 m; foragers carrying drag-producing flaps or lead weights signal greater distances than they have actually flown). The Carniolan bees used in the "cliff" experiment begin signalling distance at about 85 (horizontal) meters. In these experiments, then, it is easy to suppose that the additional effort involved in flying vertically accounts for the appearance of the distance component.

When the experiment was (almost) repeated with Italian bees (which begin to signal direction at 20 m), quite different results were obtained (von Frisch 1967a, pp. 167-168). The hive was placed on a bridge while the foragers were trained to a feeding station 76 m below. Unaccountably, the foragers performed round dances (typical of distances of less than 20 m; von Frisch suggests that the absence of a cliff for orientation accounts for the round dances. It is interesting that when Carniolan bees are

trained to a distant source and forced to dance without orientation cues, they perform disoriented waggle dances [von Frisch 1967a, pp. 134-135, 153-156]). In the complementary experiment the hive was placed at the base of a radio tower and the foragers trained to a station 50 m above. Again, the Italian bees performed round dances. (This final experiment was the only case in which the recruits did not locate the food.)

The change of both race and location confounds interpretation of these experiments, but the main point is clear: there was no variation in the dancing in any particular case (or at least none was reported). If bees were consciously attempting to adjust the old symbols to fit a new situation, some variability in the manner in which foragers decided to handle the situation might be expected. The lack of variance suggests either that the dances were governed by automatic but unknown rules without any "awareness" on the part of the bees, or that all of the bees consciously solved the problem in the same fashion.

Other examples of odd behavior come to mind, but in no case is forager variability reported. Of course, observers may simply have filtered out the differences, reporting instead the "typical" behavior. As of now, however, there is no good evidence that bees alter their dances in a "creative" way when put into rare or odd situations.

Bennett's final criterion for rationality is the ability to perform "R-denials." An R-denial is the denial of a statement not because the fact it asserts is known to be false, but because the logical basis of the statement is invalid. Consider the statement "Food is at location X because of Y." This statement could be denied because the attending bee has recently been to X and knows that there is no food there. This unlikely piece of behavior, however, does not constitute an R-denial. The same statement, Bennett points out, could be denied if the attender knows that Y does not imply that food exists at X -- that is, if it realizes that the logic is faulty.

An R-denial, then, is the denial of the logic of another's statement. Just what form either the statement or the denial might be expected to take in the case of the dance language is not clear. The "because"

implied by the forager dance might be something like "because I was just there and tasted the food." In principle, an attender could deny the logic in one of several ways. Hypothetically, the R-denial could be of the sort "you cannot be telling the truth because I know that you have not left the hive," or "you cannot have been where you say because the locale odor does not correspond to the location you are signalling," or "you cannot have been where you say because your wings have been clipped and you cannot fly," and so on. The denial need merely be a refusal to be persuaded to fly out when the dance contains a "logical error."

To my knowledge, R-denials or anything suggestive of them have never been observed in honey bees. Of course, to provide an appropriate situation for an R-denial, a forager must "lie." The absence of natural situations of this sort takes some of the force out of negative observations. In the absence of a positive search for R-denials, the possibility of their existence, however unlikely, cannot be entirely dismissed. This raises the question of just what sort of experiment could reveal whether, to any extent, honey bees might show evidence of knowing what they are about. In the case of chimpanzees, it has been the attempts at two-way communication which have suggested that a non-human species is capable of some degree of introspection. Perhaps the ability to communicate with an animal opens the most appropriate channel for analyzing, or at least inferring, mental processes. In this regard, attempts to communicate with bees by means of a model take on added significance. Perhaps only in this way will it be possible to gain a convincing insight into the mental powers of the honey bee. Considering the many remarkable abilities which have been discovered simply from observation, any attempt to probe the "mind" of the bee may well uncover new surprises.

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