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Communication of Direction by the Honey Bee

Review of previous work leads to experiments limiting olfactory cues to test the dance language hypothesis.

James L. Gould, Michael Henerey, Michael C. MacLeod

A forager honey bee, after finding a rich source of food, returns to the hive and performs a "waggle" dance which contains rather precise correlates of the distance and direction to the feeding place. On the basis of his experiments which had led to this discovery, Karl von Frisch formulated the "dance language hypothesis"—namely, that honey bee "recruits" use this information in the process of locating food (*1*). Later, Wenner (*2*) and Johnson (*3*) repeated von Frisch's work, with certain modifications, and came to the conclusion that the recruiting behavior which they observed could be explained on the basis of olfactory cues alone.

These hypotheses are not mutually exclusive; both might be applicable, in different circumstances. Simply demonstrating that olfactory cues are sufficient in a particular situation does not mean that the dance language is not used under other conditions. Since there is general agreement that the dances do occur and do contain information about distance and direction, the question is whether this symbolic information can be communicated to other bees.

The research described here was done in an attempt to test von Frisch's interpretation by means of an experimental arrangement designed to minimize or cancel olfactory cues. Only the question of information about direction is considered.

Basically, von Frisch set out stations in various directions from the experimental hive and trained bees to seek only one of them (this, in his and later work, is called the training or experimental station; the others are called observation stations). During the experiment he captured all untrained bees arriving at the several stations and found a marked preference for the direction of the training station (*1*). Johnson repeated this experiment and added a second (control) hive, in an effort to bring about "greater uniformity" among the various stations, at least with respect to the visual information conveyed by feeding bees. Control hive foragers were trained to the various observation stations, while the experimental hive bees were trained to a single experimental station. Unlike von Frisch, Johnson found that untrained bees recruited from the experimental hive showed no preference for the direction of the experimental station (*3*). Pertinent details of the two experiments are discussed below; the physical arrangements of the stations are illustrated in Fig. 1, A and B.

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Due to the many parameters inherent in the design of such experiments, including the spatial arrangement of the hive and of food sources, the training procedure, and the observation protocols, the experiments of von Frisch and of Wenner and Johnson are not sufficiently comparable to distinguish clearly between the two hypotheses. Wenner and Johnson (*2–4*) criticized several of von Frisch's procedures. Their criticisms were directed not against his original experiments in support of the "dance language hypothesis" (*1*) but against his later "step" (*5*) and "fan" (*6*) series of experiments, which *presupposed* the validity of that hypothesis. Conversely, von Frisch (*7, 8*) found fault with the experiments of Wenner and Johnson.

Many variables may affect foraging behavior, dancing, and recruitment. These are discussed below, together with the control methods used in earlier experiments. Since complete knowledge of the dynamics and relative importance of these factors is lacking, adequate controls should be used for all of them. We feel that no single previous investigator has provided such controls.

Earlier Experimental Procedures

Von Frisch used Krainer bees for his early experiments (*1*) (although in the later "step" and "fan" experiments he used bees of the Carniolan variety). Wenner and Johnson (*2, 3*) used bees of the Italian strain, as we did in our experiments.

The first step in any such experiment is to train foragers by feeding them on a sucrose solution placed at the hive entrance. The sucrose solution is gradually moved farther and farther from the hive. Von Frisch is vague about his training technique (*1*; *9*, p. 87); he seems to have trained his foragers on a 0.5*M* sucrose solution (he does not give details of the use of scent in training); with this weak solution, foraging continued, but little or no dancing occurred and no bees were recruited. Wenner (*2*) and Johnson (*3*) trained their bees on a 1.5*M* sucrose solution containing scent (for example, peppermint). This procedure presumably elicited recruitment and exposed all the bees in each colony to the experimental odor, though this is not mentioned in their reports. [In a previous experiment (*10*) this procedure elicited very little dancing (30 dances in 280 minutes) either during training or during the experiment.] Thus, even before the experiments began, the two groups of researchers were probably dealing with differently conditioned populations.

Wenner and Johnson (*2, 3, 11*) did not observe the activity of their trained foragers in the hive during the experiment. The occurrence of dancing depends not only on the sucrose concentration (*9*, p. 45) but also on unknown or poorly understood variables in the state of the hive (*9*, pp. 30, 243; *12*; *13*). It is entirely possible that their bees danced rarely, if at all (*8, 10*). Von Frisch (*1*) did not observe dancing in his series of experiments relevant to the conveying of directional information.

Olfactory and Visual Cues

A forager may carry odor back to the hive in either of two known ways, one internal, the other external. Samples of fragrant nectar from the honey stomach of the dancing forager are distributed to attending bees (*9*, p. 28). In addition, odors carried on the body of the forager (*14, 15*) are sensed by attending bees that make antennal contact with her. Von Frisch placed his feeding dishes on filter paper; during the experiments, drops of scent (aniseed, star aniseed, peppermint, thyme, or lavender oil) were placed on this paper (*1*). Thus, the foragers may sometimes have made physical contact with the source of the scent. In later experiments, von Frisch successfully used a feeding device in which the bees were separated from the source of the scent by a wire screen. Thus, any scent carried back to the hive would have been adsorbed from the air (*9*, fig. 21).

Wenner (*2*) and Johnson (*3*) used ten drops of peppermint or eight drops of lavender oil per liter of sucrose solution. Their foragers presumably returned to the hive carrying scent both in the

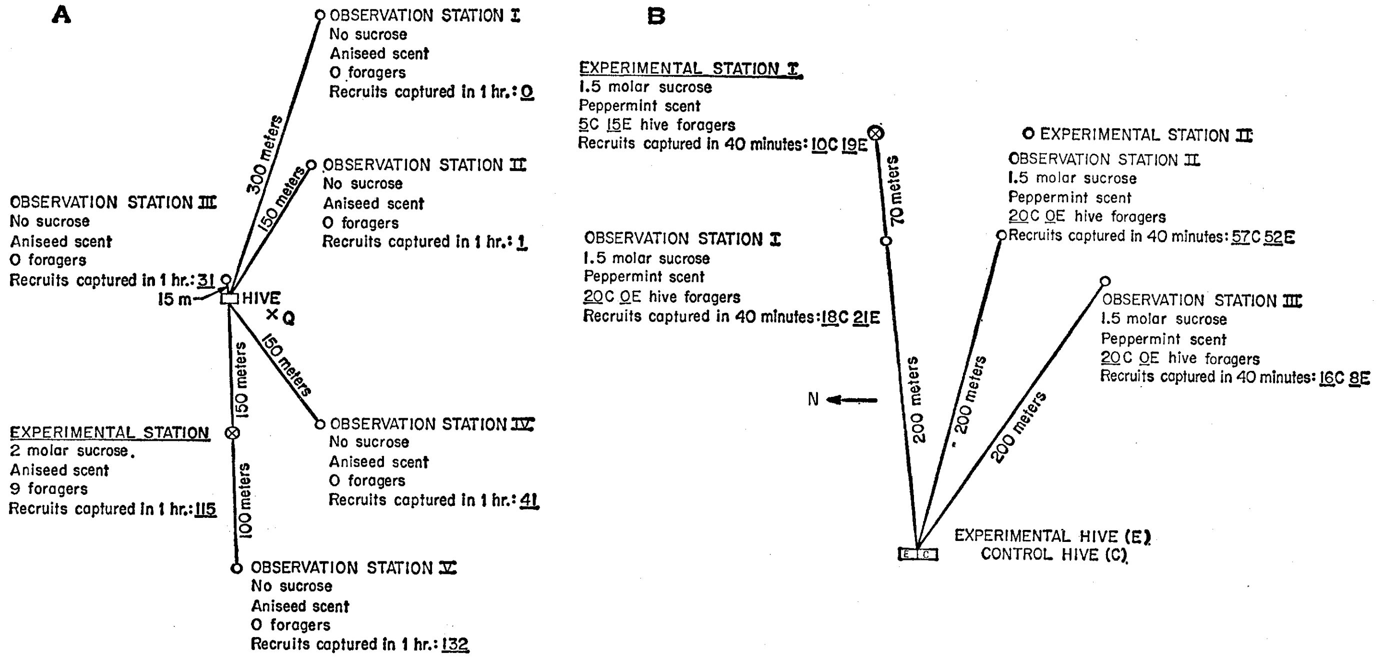


Fig. 1. Experimental arrays used previously to test the dance-language hypothesis. Pertinent information is summarized for each station. (A) After von Frisch (*1*, fig. 10). The compass and wind directions were not specified. (B) After Johnson (*3*, fig. 1).

honey stomach and on external parts of the body.

Von Frisch has suggested that bees may be able to "recognize" a particular experimenter (*9*, p. 23). Although there is little evidence that this is the case, he assumed that such recognition, if it occurs, is based on odor, some of which might be carried back to the hive and thus be available as site-specific information to potential recruits. Von Frisch did not "rotate" his observers (did not shift them from station to station) (*1*). Wenner and Johnson rotated their observers at 10-minute intervals (*2*, *3*).

For this procedure to be adequate, the observers at the feeding stations would have to be rotated frequently enough so that there would not be sufficient time between rotations for a forager to return to the hive and for one of her recruits to arrive at a feeding station. As discussed below, there is evidence that, under the conditions of our experiments, the time required for a bee to return to, land at, and enter the hive and begin to dance averages from 3 to 4 minutes (see Fig. 2). Von Frisch found that the interval between attending a dance and being observed at a feeding station 400 meters away could be as little as 1 to 3 minutes for previously trained foragers. Since we found that recruits were often able to locate the feeding station within 1 or 2 minutes after attending a dance, and since the flying time was probably less than 1 minute in all cases [the flight speed is approximately 7 meters per second (*16*)], it is possible that, on a 10-minute rotation schedule, a given observer could be present at a station during both the visit of a forager and the arrival of its recruits (*17*). Although possibly not important in Johnson's experiments, the adequacy of 10-minute rotation of observers is subject to question.

Various odors may accumulate at the feeding stations, in the air, in the sucrose solution, and on the feeding device holding the sucrose solution. Wenner (*2*) and Johnson (*3*) "rotated" their feeding devices every 10 minutes. Von Frisch did not consider the possible long-distance effects of odors, except in the case of the scent of the Nasanov gland.

The honey bee has a scent-producing organ, the Nasanov gland, located at the rear of its abdomen; under certain circumstances bees will evert this organ and fan their wings, thus releasing its scent into the air (*9*, p. 50). It has been shown (*14*) that the presence of Nasanov gland odor increases visitation and recruitment in the vicinity of the odor. In his experiments on directional information von Frisch performed a control experiment in which the scent organs of the foragers were sealed, and he found that the directional pattern of recruitment was unchanged (*1*). Unfortunately, this control experiment was performed at a site previously rejected because "the different directions were dissimilar" (*1*). Therefore, other cues could have accounted for the directional effects observed.

Wenner and Johnson used foragers from a "control hive," which visited each of their observation stations in equal numbers (see Fig. 1B). However, the experimental station was frequented for the most part by bees from the experimental hive, so that if there were differences in the condition of the two colonies that affected the rate at which their members exposed their scent organs, an imbalance in this respect between the experimental and observation stations could have been introduced.

On the average, bees do not expose their scent organs until their sixth visit to a site (*18*). We observed no exposure prior to the third visit. Since, in all the experiments, recruits were captured on their first visit, one may assume that recruits did not contribute to the level of the Nasanov gland odor.

Several investigators have noted that bees are able to distinguish food sources visited by members of their own colony from sources visited by members of another hive (*19*, p. 228; *20*). It is further reported that hive odor accumulates at a station and makes it more "attractive" to recruits from that hive (*21*).

In von Frisch's experiments (see Fig. 1A) hive odor was present only at the experimental station. The assumption seems to have been that any such odor at the experimental station is entirely local and thus has no influence on recruitment to the other stations. Wenner and Johnson provided hive odor at all stations through their use of a "control hive" containing mutant bees, distinguishable by their different body color (Fig. 1B). One should consider the possible importance of differences in hive-specific odor to foraging, dancing, and recruiting behavior. This factor might be particularly relevant at the experimental station, where bees from both the experimental and the control hives foraged. Because the effects of this factor are uncertain, the value of Wenner's and Johnson's rotation of the feeding dishes at 10-minute intervals is difficult to assess.

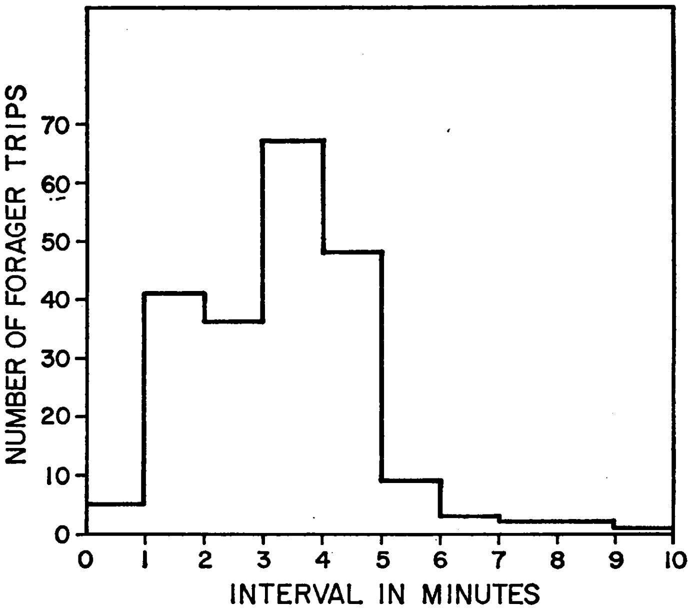
Recruits tend to land more often where there are other bees; small bee-sized pieces of sponge have been used to increase the landing rate at less-frequented stations and decrease the visual difference between stations (*11*). Von Frisch provided no such "encouragement" at his observation stations. Wenner and Johnson used foragers from their "control hive" to encourage landing; in order to easily identify the hive to which an individual bee belonged, they used mutants of a different body color for the control colony (*2*, *3*). The possible visual effect, if any, of body color cues upon potential recruits is not known.

Capture of Recruits

To eliminate the possibility of recruits' returning to the hive and recruiting others, or being counted at the stations more than once, recruits were captured upon arrival at the experimental and observation stations. The exact method of capture is important, since, under certain circumstances, bees will expose their stings, releasing an alarm odor (*19*, p. 230). One of the effects of this odor is to induce other bees to sting moving objects in the vicinity. Von Frisch originally caught all recruits with forceps, a technique that caused the captured bees to release the alarm odor (*1*). Later, von Frisch began to "gently" transfer the bees into alcohol, but he does not describe the exact technique. Wenner and Johnson picked up the recruits by their wings and placed them in a jar of alcohol (*22*). When we captured bees by this last method, they exposed their stings before they could be placed in alcohol. The odor of alcohol released into the air around the experimental and observation stations in both groups of experiments is another uncontrolled variable. As described below, it is possible to capture bees without the release of these odors.

Symmetry

In von Frisch's experiments (Fig. 1A) and in Johnson's (Fig. 1B), the array did not provide for symmetry with respect to many factors pertaining to the hive, the wind, or features of the landscape.



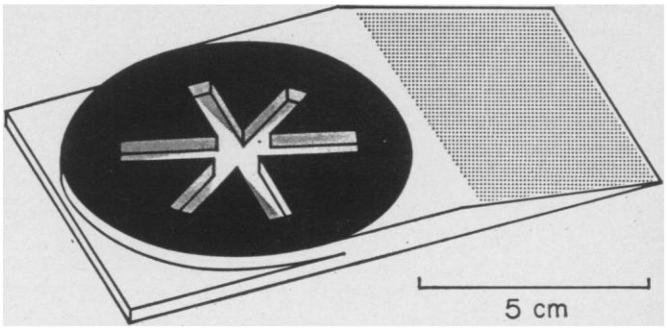


Fig. 2 (left). "Forager delay"—the time interval from observation of a numbered bee beginning to feed to observation of the same bee dancing in the hive. The distribution represents 214 visits (involving, in all, 43 series 1 foragers). Fig. 3 (right). Training device, constructed of a solid piece of balsa wood with six radial grooves, each cut to a depth of 4 millimeters. For visual recognition, the insides of the grooves were painted flat blue and the top of the disk was painted flat black. The grooves were filled with sucrose solution.

Wind is undoubtedly an important factor; not only does it displace odors but it may also affect a recruit's search pattern (*16*). One should also consider possible olfactory and topographic irregularities of the site. Many experiments related to the controversy have been carried out in or through orchards (*9*, p. 153), lakes and cities (*1*; *9*, p. 152), tree lines (*2*), and other features which could provide visual and olfactory landmarks. Bees are quite responsive to such cues (*23*; *9*, pp. 331 and 186); an ideal site would be devoid of them.

In each of the cases discussed above, assumptions seem to have been made concerning what is or is not "important" to the bees. Without careful control experiments or design to cancel or limit possible biasing effects, completely objective conclusions are not likely to be reached.

Preliminary Experimental Procedures

Two series of experiments designed to provide such controls were recently performed. In the series 1 experiments most of the bees in the hive were individually numbered, as described below, while in the series 2 experiments they were not. Two colonies of Italian strain honey bees (*Apis mellifera ligustica*) were used. In series 1 a colony of 8000 to 10,000 bees was used (*24*); in series 2, a colony of 6000 to 8000 bees (*25*). These colonies, though obtained from different suppliers, had queens derived from the same apiary (*26*). The age of each colony assured that all of its members were the progeny of the current queen.

For the series 1 experiments, approximately 5000 bees were tagged (*27*). The 2200 distinct markers used were such that the probability of confusing two bees carrying the same marker in any one experiment was negligible. The tagging was accomplished by chilling bees in groups of 25 to 50 to quiescence and glueing a tag (*27*) to the thorax of each bee. The group was then returned to the hive entrance. By the time the bees became active the glue had dried and the tags were firmly attached.

Both colonies were kept in observation hives (52.8 by 62.9 by 7.0 centimeters) containing two "brood frames" and one "shallow frame." The hives were designed and built at the California Institute of Technology. The entrance was so located that incoming bees were forced to enter and walk on the "front" side of the hive, where dancing could be observed (*9*, p. 7).

Training

Training was accomplished by a modification of Gary's technique (*28*). To leave the hive, the bees had to walk onto a wooden training-feeder device, consisting of a disk with a radial arrangement of grooves (see Fig. 3); the device contained (in the grooves) 3 milliliters of 2.5*M* sucrose scented with orange oil (ten drops per liter) (*29*). As the bees began to frequent this device, it was gradually moved away along a board 2 meters long which extended from the hive entrance. Beyond about 0.5 meter the foragers (30 to 40 in number) began to fly to the device rather than to walk to it. At 1 meter from the hive the device was removed and replaced by a table on which was placed a feeding station (see Fig. 4). (This portion of the training initially consumed an hour or more, but later it required less time, sometimes as little as 10 minutes.) The feeding station consisted of a concave wooden mold covered by a disposable polyethylene sheet (Fig. 4); in the depression was placed sucrose solution (10 milliliters) on which was floated a feeding disk visually and functionally identical to the training device (the grooves were cut through the disk, thereby exposing the sucrose on which the disk floated). At this stage of training, orange-scented 2.5*M* sucrose was still used. At 2 meters from the hive a second table with feeding station was added, adjacent to the first, and training proceeded simultaneously in opposite directions.

Beyond 10 meters, "as the bee flies," training was completed with orange-scented 0.5*M* sucrose, a molarity which, according to our observations, produced very little dancing and elicited almost no recruits. In the series 1 experiments, any unnumbered foragers were captured and discarded. In the series 2 experiments, all the foragers were marked with numbered tags while feeding. (When bees feed they are very single-minded and show no great reaction to such manipulations as tagging and painting.)

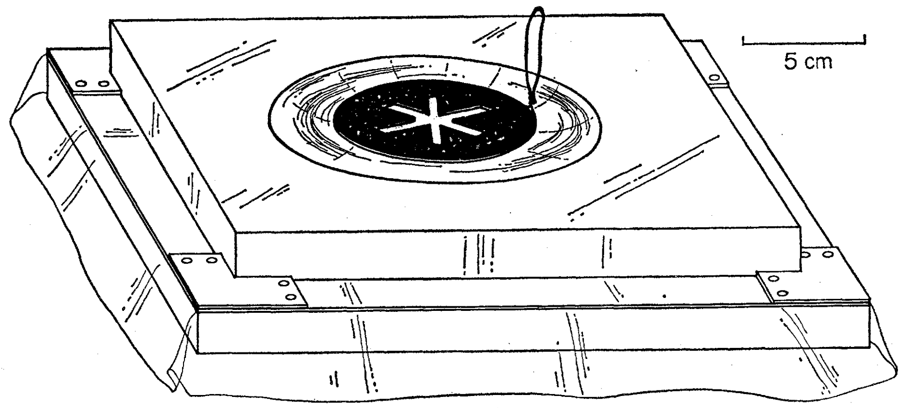


Fig. 4. Feeding station, constructed of a hardwood block with a depression in the top. The device was covered with a disposable plastic sheet held down by a square metal frame. Sucrose solution (10 milliliters) was placed in the depression and a balsa disk ⅛ inch (0.38 centimeter) thick was floated on the surface of the solution. For visual recognition, this disk was painted flat black and, like the training device, had six radial grooves painted blue. The disk had a wire handle to allow manipulation without touching the sucrose. The station was supported by a tubular-frame stand; the top of the disk was 72 centimeters above the ground.

When a feeding station was at 120 meters from the hive, the first foragers to arrive (10 or 15, as specified) were defined as that station's "foraging group," and all foragers arriving subsequently were captured. To facilitate later recognition of the members of the foraging groups, all these bees, for both the series 1 and the series 2 experiments, were marked on the abdomen with small dots of lacquer-base paint very early in the training procedure. A different color was used for each station. In the case of the series 2 bees these dots were placed at the rear of the abdomen in such a way as to seal the Nasanov gland. The Nasanov gland seals were checked during each future visit of a forager to a station; when the seals cracked, as occasionally they did, they were repaired.

At the conclusion of training, the two feeding stations were 180 degrees apart and equidistant from the hive, and each was supplying its foragers with orange-scented 0.5*M* sucrose solution. Approximately 5 minutes before the experiment proper was to begin, the sucrose solution used in training was removed and fresh sucrose solution (0.5*M*) containing the experimental scent (if any) was substituted for the solution used in training. The plastic sheet and feeding disk used in training were temporarily left in place, since, when everything was changed simultaneously, foragers showed reluctance to land and continue feeding. All the experiments were performed between 2 and 6 p.m. Pacific Daylight Time.

Procedure at Feeding Stations

As the experiment started, the solution and plastic sheet used in training were discarded into an airtight plastic bag and replaced by a new plastic sheet and 10 milliliters of the experimental solution. The feeding disk used in training was retained, to maintain continuity of foraging. All sheets and solutions at the various stations were replaced every 10 minutes, the used material being sealed each time in an airtight plastic bag. In the series 1 experiments the same feeding disk, rinsed after 5 minutes, was used at a given feeding station throughout the experiment; the observers were rotated every 10 minutes. In the series 2 experiments the feeding disks were rotated when the observers were, at 5-minute intervals, being carried from one station to the other in plastic bags. The training disks were replaced by clean disks at the time of the first rotation. Since bees are easily distracted by the presence of people between the feeding station and the hive, the observers, when going from one station to the other, followed a path at least 40 meters from the road on which the feeding stations and the hive were located.

To preclude spillage, the sucrose solutions were taken from bottles with skirt-type rubber stoppers by means of syringes and needles.

At each station there was a tape recorder into which was read the time (to calibrate later transcription); the number of arrivals (foragers and recruits); identification numbers, if any; and any other pertinent data. All recruits (bees not among that station's official foraging group), including any previously trained but unlisted foragers, were captured. Only recruits not previously trained as foragers were counted in the data. It was found that, when a plastic bag was placed over a bee as it was feeding, the bee would invariably walk up the side of the bag, exhibiting no alarm, and could be sealed in. This procedure precluded the release of alarm odor into the air. Official foragers were not captured; no recruits were permitted to return to the hive.

Communication among the observers, including the hive observer, was maintained by walkie-talkie.

Table 1. Data on "foragerless control" experiments of 12 August 1969. Bees from the colony of numbered bees (see text) were used. Sucrose (2.5*M*) scented with peppermint was offered for 2 hours at each of two stations equidistant from the hive but in opposite directions from it. All the arriving bees were captured and counted, and their identification numbers were recorded. No previously trained foragers were included in the count. Recruitment under these conditions was negligible.

Weather						Direction of station	Recruits (*N*)
Sky	Average wind direction	Average wind speed (mile/hr)	Average temperature (°C)	Average humidity (%)	Atmospheric pressure (mm-Hg)		
			Experiment No. A1				
Sunny, clear	NW	7–10	24.6	34	655	N	1
						S	0
			Experiment No. A2				
Sunny, clear	W	5–10	26.1	40	655	E	0
						W	0

Hive Observation

Two hive observers (inside the observation shed) recorded the dances of marked foragers, together with the forager identification number, the time at which the dance occurred, its direction, and the identification numbers, if any, of attending bees. If a bee was observed to maintain antennal contact with a forager through three or more consecutive cycles of a dance, it was scored as an "attender." The number of untagged "attenders" was also recorded. The first observer called out this information, while the second observer recorded it. This second observer also took readings every 10 minutes of wind speed, wind direction (the direction from which the wind came), temperature, and humidity and periodically checked the far side of the hive to make sure that there was no dancing there. None was ever observed.

The hive was located in a fiberboard shed (1.2 by 1.2 by 2.4 meters) upon which were mounted an anemometer and wind vane (elevation, 3 meters), a thermometer, and a humidity-measuring device. Atmospheric pressure was obtained from the local weather bureau (*30*). The hive opening extended through the south wall of the shed, 0.72 meter above the ground.

Environment

The experimental site (*31*) was located in the high desert (elevation, 1275 meters) near Burns, Oregon. The area was flat (to within ± 1 meter) for at least 1 kilometer in all directions. For at least 7 kilometers in all directions the vegetation consisted almost entirely of dry sagebrush (*Artemesia tridentata* and *A. arbuscula*), crested wheat and squirreltail grass (*Agropyron cristatum* and *Sitanion hystrix*), and "rabbit brush" (*Chrysothamnus vicidiflorus* and *C. nauseosus* (*32*). Apparently there was no local source of nectar, due perhaps to the low humidity and the nature of the vegetation. The bees consumed all the liquids offered and, when not fed, rapidly depleted their store of honey. They found adequate supplies of pollen, largely among the dry rabbit brush, and were supplied continuously with water by the experimenters.

Training proceeded along dirt roads that intersected at the hive (see Fig. 5), one of which (the easterly road) was built especially for these experiments. These paths offered no detectable asymmetries, either olfactory or visual. A survey of the vegetation showed that there was in fact uniform distribution of plants in all directions.

Experiments

"Foragerless control." The purpose of the "foragerless control" experiment was to determine the rate at which untrained bees arrived at each of two stations when no active foraging was in progress. Sucrose solution (2.5*M*) with peppermint scent (ten drops per liter) (*29*) was offered at two stations 180 degrees apart and each 150 meters from the hive. All arriving bees were caught and recorded. The data were edited so as to exclude foragers trained on previous days, who thus "knew" the location of the feeding station. The results are shown in Table 1. When no active foraging was in progress, only one naive recruit was found in 8 hours of observation.

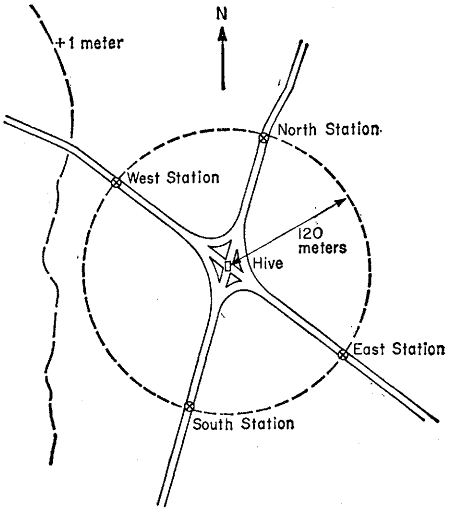


Fig. 5. The experimental site. Experiments were performed on a dry, flat area (see text). The contour line indicates an elevation of 1 meter with respect to the hive. The orientation of the dirt roads along which the training took place is shown. The north-south road ran 12 degrees east of north, while the east-west road ran 28 degrees north of west.

"Danceless control." The purpose of the "danceless control" experiment was to determine the rate at which recruits arrived at each of the two stations when active foraging was in progress, but when little or no dancing was taking place in the hive. This determination was made as follows. After 30 bees had been given standard training as foragers, 15 for each station, weak (0.5*M*) sucrose solution was offered at both stations. An observer in the shed verified that, under these conditions, little dancing occurred. Any dancing that did take place was recorded. All visits of bees to the stations were recorded, and all recruits were captured. The experiment was performed three times, once with peppermint scent and twice without scent but with different aspects of the experimental configuration to the wind. The results are shown in Table 2.

In all cases, very little recruiting occurred; this was true with or without scent, and regardless of the direction of the wind when no scent was used. Overall, there were 1461 visits by foragers, 70 dances, and only eight recruits. The total recruiting efficiency (the ratio of

Table 2. Data on the "danceless control" experiment. Bees from the unnumbered-bee colony that had received standard training as foragers (see text) were used. A weak sucrose solution (0.5*M*) was offered to ten trained foragers at each of two stations equidistant from the hive but in opposite directions from it, to encourage foraging not followed by dancing. All arrivals were recorded and all recruits were captured. The experiment was performed three times (on 31 August and 5 and 7 September 1969), once with peppermint (P) scent and twice without scent. In one of the experiments in which no scent was used, the wind was generally parallel to the line of flight from hive to station; in the other two experiments it was generally at right angles to the line of flight. Recruitment in the absence of dancing was quite low.

Weather						Duration of experiment (min)	Direction of station	Scent	Forager visits (*N*)	Dances (*N*)	Recruits (*N*)
Sky	Average wind direction	Average wind speed (mile/hr)	Average temperature (°C)	Average humidity (%)	Atmospheric pressure (mm-Hg)						
				Experiment No. B1							
Sunny, clear	WNW	5–8	24.3	35	653	120	N S	P P	279 208	5 6	3 2
				Experiment No. B2							
Partly cloudy	E	4–10	31.0	30	656	60	N S	None None	168 160	13 13	0 0
				Experiment No. B3							
Sunny, clear	ESE	3	31.1	19	657	120	N S	None None	304 342	21 12	2 1

Table 3. Data on series 1 experiments (recruitment when there was dancing by foragers). Bees from the numbered-bee colony that had received standard training as foragers were used. A 2.5*M* sucrose solution was offered to ten trained foragers for 2 hours at each of two stations equidistant from the hive but in opposite directions from it. All arrivals were recorded and all recruits were captured. The experiment was performed three times (on 15, 16, and 18 August 1969), once with peppermint (P) scent and twice without scent. In one of the experiments in which no scent was used, the wind was generally parallel to the line of flight from hive to station; in the other two experiments it was generally at right angles to the line of flight. In the series 1 experiments recruitment was significantly higher than it was in the control experiments.

Weather										
Sky	Average wind direction	Average wind speed (mile/hr)	Average temperature (°C)	Average humidity (%)	Atmospheric pressure (mm-Hg)	Direction of station	Scent	Forager visits (*N*)	Dances (*N*)	Recruits (*N*)
				Experiment	*No. C1*					
Sunny, clear	NW	5–10	27.0	29	654	N	P	344	60	37
						S	P	298	63	52
				Experiment	*No. C2*					
Sunny, clear	W	8–12	30.8	33	652	N	None	292	57	87
						S	None	194*	53	35*
				Experiment	*No. C3*					
Sunny, clear	W	6	30.4	28	650	E	None	198	7	4
						W	None	247	18	10

* Thirty minutes of data were lost.

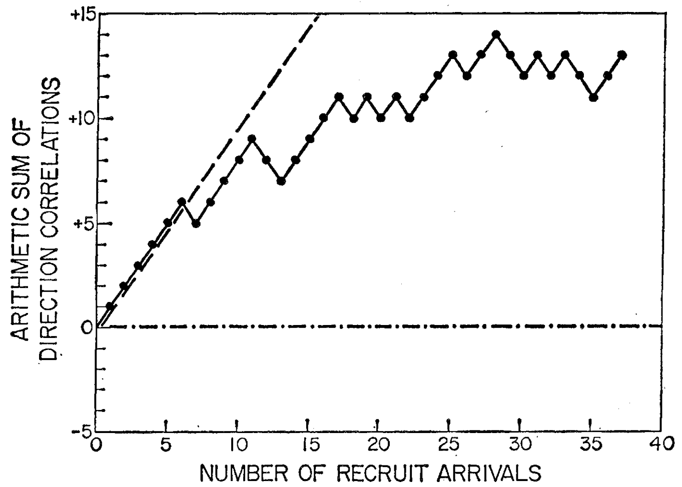
recruits captured to forager dances observed) was 0.11.

Series 1. The series 1 experiments were designed to examine the behavior of individual recruits as each attended a dance and subsequently arrived at a feeding station. By comparing the direction specified by the dance attended by a recruit with the direction of the station at which the same recruit was later caught, one should be able to determine the degree to which the recruit used the dance information. If the two food sources were identical with respect to odor, and if only olfactory cues were being used, one would expect recruits to find the two stations with equal frequency, irrespective of the direction indicated by the dance they attended. If, on the other hand, dance-language information was being utilized by the recruits, a higher correlation with the direction indicated by the dance would be expected. By making complete observations in this way, one may also determine the interval between dance attendance and capture.

After standard training such that ten foragers frequented each station, 2.5*M* sucrose (unscented or with peppermint scent) was offered at both locations. All arrivals were recorded, and all recruits were captured. The results are shown in Table 3.

The experiment was performed three times, once with peppermint scent and twice without scent; results of experiments in which no scent was used can be compared in order to check for any effects of the wind. With the more concentrated sucrose used in this experiment, the dancing rate greatly increased; furthermore, the recruitment rate was much higher than in the danceless control experiment. Altogether, there were 1573 forager visits, 258 dances, and 225 recruits; the recruiting efficiency was 0.87.

Of the recruits, 37 which had been numbered were observed attending a dance in the hive. In Table 4, the time of the dance attended and its direction are compared with the time the recruit was captured and the direction of the station. Table 4 lists the bees in order of increasing intervals between dance attendance and capture and indicates whether the dance and capture directions are the same (plus correlation) or opposite (minus correlation).



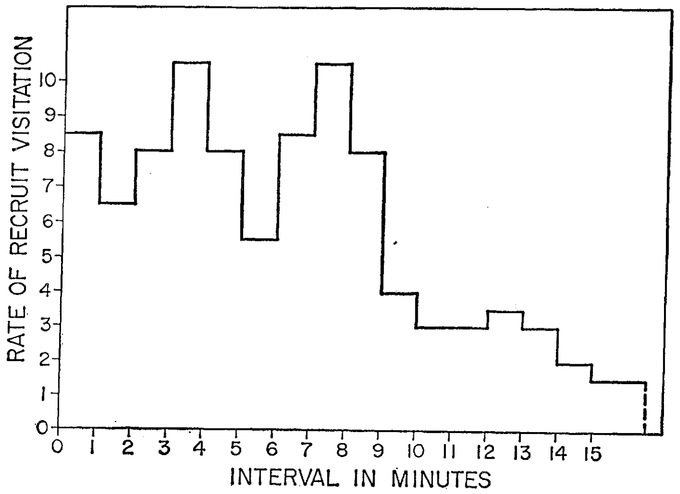


Fig. 6 (left). Direction correlations. The scale on the ordinate represents the arithmetic sum of direction correlations (a positive correlation is counted as +1 and a negative correlation, as −1); the scale on the abscissa arranges the arrivals in order of increasing intervals between dance attendance and capture (taken from series 1 data given in Table 4). Also plotted are the curves expected from (dashed line) a 100 percent positive correlation and from (dot-and-dashed line) a random (50 percent) correlation. Fig. 7 (right). "Recruit delay"—the time interval from observation of a numbered bee attending a dance to capture of the same bee at a feeding station. The distribution represents 65 recruits from series 1 and related experiments.

For short intervals, most correlations are positive; for longer intervals, negative and positive correlations appear with equal frequency. These data are plotted in Fig. 6.

In this experiment, the average delay between a forager's feeding at a station and dancing in the hive was 3 to 4 minutes (these results are plotted in Fig. 2), whereas delays between the recruits' dance attendance and arrival at a feeding station were distributed almost uniformly from < 1 minute to 9 minutes (these results are plotted in Fig. 7).

Series 2. In the series 2 experiments we used different concentrations of sucrose at the two stations (experimental and control stations) so that only one group of foragers danced; otherwise the stations were identical. We then counted the arrivals at each station. The object was to learn whether dance-language was being used. If dance language was not being used, one would expect to find recruits at the two stations in equal numbers; on the other hand, if such information was being used, one would expect to find more recruits at the station indicated by the dancing in the hive.

After standard training of foragers, 1.0*M* sucrose was offered at the experimental station while 0.5*M* sucrose was offered at the control station. To obtain similar rates of forager visitation, ten of the foragers in the experiment were trained to frequent the experimental station, 15 foragers were trained to frequent the control station [the visitation rate per forager was higher at the station which offered sucrose of higher molarity (*9*, p. 251)]. The dancing observed in the hive predominantly indicated the experimental station (93 percent). At both stations the sucrose solution was either unscented or peppermint-scented, as specified. All arrivals were recorded and all recruits were captured. The results are shown in Table 5.

To eliminate artifacts due to site taxis, each experiment consisted of two parts which differed only in that the locations of the experimental and control stations were reversed. Each two-part experiment was performed three times, once with peppermint scent at both stations and twice without scent. Overall, there were 924 forager visits at the experimental stations and 994 at the control stations. The control-station foragers showed a recruiting efficiency of 0.36, and the experimental-station foragers, an efficiency of 0.54.

Observations at the hive revealed 526 dances indicating the experimental stations and 36 dances indicating the control stations. In all, 295 recruits were captured; of these, 282, or 96 percent arrived at the experimental stations.

Station Equivalency

The validity of these results depends upon the success of our efforts to make the stations in every way equivalent. In Table 6 these efforts are summarized and compared with earlier work. The similar rates of forager visitation at the two stations presumably kept the amounts of hive-specific odor, the degrees of visual landing-encouragement, and (in series 1 experiments) the quantities of Nasanov gland odor approximately equal. The apparent uniformity of the landscape should have limited or eliminated site- and path-specific odors. General site taxis was controlled internally in series 1 experiments and controlled through reversal of the experimental and control stations in series 2. By utilizing various aspects to the wind in each series, the effect of such orientation could be studied. Sealing of the Nasanov gland in the series 2 experiments precluded release of that odor, while the capture technique prevented release of the alarm odor. Disposal of the experimental materials into airtight plastic bags every 10 minutes and the rotation of experimenters and feeding disks prevented development of differences relating to these factors between the stations as the experiment progressed. In the series 2 experiments the rotation of observers should have removed any bias relating to an individual observer.

Observation of the hive allowed us to record most of the dancing, and, later, to compare behavior of the foragers and recruits in the hive with that observed at the feeding stations.

Table 4. Data on series 1 experiments. Data recorded at the feeding stations and observations at the hive were compared to find which numbered recruits had also been observed attending a dance. Data from all series 1 experiments (Table 3) were pooled. Listed below, for each numbered recruit, are the time of the dance attended and the time of capture, the direction specified by the dance attended ("dance direction"), the direction of the station at which capture occurred ("capture direction"), the interval between dance attendance and capture, and the correlation (positive or negative) of dance direction with capture direction. The listings are arranged in order of increasing time intervals (column 7), and the sources of the data are given (columns 1 and 2). For the shorter intervals, positive correlations predominate: correlation totals for intervals of less than 4 minutes are 10+, 1−; for intervals of less than 15 minutes, 21+, 7−; for intervals of less than 90 minutes, 25+, 12−.

Bee number	Experiment number	Dance time (p.m.)	Capture time (p.m.)	Dance direction	Capture direction	Time interval (min)	Direction correlation
Y41R	2	3:43	3:43	N	N	< 1	+
B94W	3	3:12	3:12	E	E	< 1	+
B65G	3	3:59	4:00	W	W	1	+
R02W	3	4:24	4:25	W	W	1	+
B27R	2	3:14	3:16	N	N	2	+
B07B	2	3:53	3:55	N	N	2	+
R12W	2	4:06	4:08	N	S	2	−
R71R	2	4:24	4:26	S	S	2	+
W04B	1	5:06	5:09	S	S	3	+
G88G	1	5:06	5:09	S	S	3	+
W09G	3	3:25	3:28	W	W	3	+
W95B	1	4:51	4:55	S	N	4	−
Y70B	2	4:19	4:23	N	S	4	−
Y16G	2	3:43	3:49	S	S	6	+
B10Y	2	4:48	4:54	N	N	6	+
W24W	2	4:25	4:32	S	S	7	+
B68Y	2	4:48	4:55	S	S	7	+
W10B	2	4:55	5:02	N	S	7	−
B92B	1	5:42	5:50	N	N	8	+
Y51G	2	4:29	4:37	S	N	8	−
Y79G	2	4:47	4:55	N	N	8	+
B39G	1	5:15	5:24	S	N	9	−
R05Y	2	5:26	5:36	N	N	10	+
R03Y	2	4:24	4:35	S	S	11	+
Y08G	1	4:10	4:22	S	S	12	+
B50Y	1	5:00	5:13	S	N	13	−
R33G	2	4:36	4:51	S	S	15	+
B70B	3	3:24	3:39	W	W	15	+
Y49Y	1	4:38	5:01	S	N	23	−
W27B	2	3:40	4:03	N	S	23	−
G63G	2	3:59	4:24	S	S	25	+
B09W	1	4:12	4:37	S	N	25	−
W80B	2	4:06	4:35	N	N	29	+
W94B	2	3:49	4:19	S	N	30	−
W82Y	1	4:37	5:08	N	S	31	−
W49G	1	4:04	5:03	S	S	59	+
B81Y	1	4:29	5:44	S	S	75	+

Some Implications of the Results

The "foragerless control" experiment showed virtually no visitation by bees when no active foraging was in progress (see Table 1). The "danceless control" experiment showed very little recruitment when there was little or no dancing (see Table 2).

The results of our series 1 experiments indicate that the degree of correlation between the direction of the station at which a particular recruit was captured and the direction indicated by the dance attended by the same recruit is apparently related to the interval between dance attendance and capture. Of the 11 recruits caught within 4 minutes of dance attendance, ten were captured at the station which had been indicated by the dance. Of the 12 recruits caught 12 or more minutes after dance attendance, only six were captured at the station indicated by the dance (see Fig. 6)—the number one would expect on the basis of random choice. Possibly there was some loss of information with time. Another possibility is that the bees that arrived after longer intervals might have attended other dances later on without being observed. Of course, if there were any bees incapable of using dance information, they would probably require more time, on the average, to discover a food source.

In the series 2 experiments, an overwhelming majority of the recruits were captured at the experimental stations regardless of the scent used and regardless of the direction of the stations or of the wind. The small number of recruits at the control station was roughly related to the low rate of dancing for that station. Calculation of the statistical significance of this experiment depends upon formulation of a hypothesis regarding the extent to which bees depend on olfactory cues in finding a food source. Suppose the recruits did not utilize the directional information given in the dance; then, half of them (148) would be expected to arrive at each of the two stations. Under this supposition, the probability that 282 out of 295 recruits would arrive at a single food source, as was the case in our experiments, is extremely small.

Efficiency of the Dance

The recruitment ratios (0.9 with 2.5*M* sucrose and 0.5 with 1.0*M* sucrose) may, at first sight, seem to be low. In the series 1 experiments we found that two naive numbered bees, on the average, attended each dance (that is, 277 different bees attended 155 observed dances). Only 37 (that is, 13 percent) of these 277 attendants were successfully recruited and later caught at a feeding station, even though the high molarity (2.5*M*) of the sucrose used reportedly produces maximum dancing and recruitment [see (*13*); unfortunately, von Frisch does not report the efficiencies he observed]. The percentage of dance-attenders that were stimulated by the dance to search for the food must, of course, have been higher than 13 percent. Although an individual bee may not be particularly good at locating a food source, the efficiencies observed indicate that, once a source is found by foragers, it can be exploited very effectively. So long as the source remains a good one, new recruits will recruit still other new bees, and this provides a cascade effect. Even with a recruiting ratio of 0.5 recruit per forager dance and a round-trip time of 5 minutes, the number of bees foraging at a particular source would increase tenfold within 30 minutes.

Conclusion and Summary

In the presence of controls for site- and path-specific odors, observer and food-source scents, Nasanov gland and alarm odors, visual cues, wind, and general site taxis, recruited bees were able to locate the food source indicated by the dances of returning foragers in preference to a food source located at an equal distance in the opposite direc-

Table 5. Data on series 2 experiments (recruitment when dances predominantly indicate one station) performed from 1 through 7 September 1969. Bees from the unnumbered colony that had received standard training as foragers were used; 1.0*M* and 0.5*M* sucrose solutions were offered at the experimental and control stations, respectively. Each of the three experiments consisted of two parts in which the directions of the experimental and control stations were reversed. In one of the three experiments, peppermint (P) scent was used; in the other two, no scent was used. In one of the two experiments in which no scent was used the wind was generally parallel to the line of flight from hive to station; in the other two experiments it was generally at right angles to the line of flight. The sky was sunny and clear during all experiments except No. D2b when the sky was cloudy. Ninety-six percent of the recruits arrived at the station indicated by 93 percent of the dancing.

Weather					Duration of experiment (min)	Scent	Direction of experimental station	Direction of control station	Forager visits (*N*)		Dances (*N*)			Recruits (*N*)	
Average wind direction	Average wind speed (mile/hr)	Average temperature (°C)	Average humidity (%)	Atmospheric pressure (mm-Hg)					Experimental station	Control station	Experimental station	Control station	Total	Experimental station	Control station
						Experiment No. D1a									
W	3–7	28.5	30	657	90	P	N	S	127	163	93	17	110	77	1
						Experiment No. D1b									
NW	5–8	24.1	24	653	120	P	S	N	245	200	95	2	97	21	1
						Experiment No. D2a									
E,W	1–3	27.3	31	657	60	None	N	S	93	132	80	0	80	62	0
						Experiment No. D2b									
E	5	31.5	30	655	60	None	S	N	138	140	101	0	101	64	0
						Experiment No. D3a									
SSW	3–7	28.4	30	657	60	None	S	S	101	133	82	2	84	59	0
						Experiment No. D3b									
SSW	5–9	34.0	16	655	120	None	N	N	220	226	75	15	90	69	11
Totals													562	352	13

tion. This was true even when foragers were simultaneously dancing to indicate two different stations. Recruitment in the absence of dancing was very low, while in the absence of foraging it was virtually zero. Thus, under the experimental conditions used, the directional information contained in the dance appears to have been communicated from forager to recruit and subsequently used by the recruit.

However unlikely it may be, one cannot rule out the possibility that recruits use some factor other than either the dance information or the possible olfactory and visual cues for which we established controls. 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 the attenders. Using polarized light, for example, to reorient the dance (*13*) would not work because the attendants observing the modified dance would themselves be reoriented by the modified conditions and, on leaving the hive, would correctly orient with respect to the polarized light of the sky.

It must also be pointed out that our experiments do not eliminate the possibility that, under certain circumstances, odor cues alone might suffice. There is evidence that bees make use of light, gravity, odor, and an internal clock system in their food gathering behavior. Our experiments appear to confirm von Frisch's contention that the directional information contained in the forager's waggle dance does, indeed, convey additional information which can be utilized by recruits.

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17. The probability of such an overlap, as calculated on the basis of data given in Figs. 2 and 7, is 66 percent. If one assumes that the observer odor "lingers" as the observer

Table 6. Relevant parameters of series 2 experiment are compared with those of previous work.

Item	Von Frisch[*]	Johnson[†]	Caltech (series 2)
Colony			
Size	Not stated	20,000	6000–8000
Race	"Krainer"	Italian; cordovan mutant in control hive	Italian
Training			
Strength of training solution	0.5*M*	1.5*M*	0.5*M*
Training scent	Not stated	Same as experimental	Different from experimental
Recruits elicited?	Few	Not stated	Few (all caught)
Observation			
Are dances observed?	No	No	Yes
Are recruits caught?	Yes	Yes	Yes
Capture method	Not described, placed into alcohol	Picked up by wings, placed into alcohol	Sealed in plastic bags
Rotation			
Observers	No	Each 10 minutes	Each 5 minutes
Materials (feeding devices, solutions)	No	Each 10 minutes	Each 5 minutes, or replaced each 10 minutes
Odor			
Experimental scent	On filter paper, "replenished frequently"	In feeding solution, 10 drops per liter	In feeding solution, 10 drops per liter
Nasanov gland	Glands sealed in control only (experiment performed at site previously rejected)	Control foragers at observation stations	Glands sealed
Hive odor	Present at feeding station only	Control odor at all stations; experimental odor at experimental station[‡]	Present at both stations, equal visitation rate
Symmetry			
Site	Aich, Germany; open grassland, orchard near[§]	Santa Barbara, Calif., football practice field	Eastern Oregon desert; flat, dry, regular
Distance of stations (meters)	Experimental: 150; observation: 15, 150, 250, 300	Experimental: 270; observation: 200	120
Prevailing wind direction	Not stated	140°[‖]	Deliberately varied[¶]
Control of site taxis	Experimental stations varied 160°	Experimental station varied 20°	Experimental station varied 180°
Center of odor			
Hive (not including hive itself)	At experimental (feeding) station only	Experimental: experimental station; control; 7 m NNE of middle station	At hive
Nasanov gland	At experimental station	30 m NNE of middle station	At hive
Experimental scent	See Fig. 1B: point Q	30 m NNE of middle station	At hive
Miscellaneous			
Concentration of experimental solution	2.0*M*	1.5*M*	1.0*M*
Visual landing encouragement	At experimental station only	Control foragers at observation stations	Equal foraging at each station

[*] See (*1*). [†] See (*3*). [‡] Dishes rotated. [§] See (*9*, p. 155). [‖] See (*3*, table 1). [¶] See Tables 1–3 and 5.

is shifted to another station, then the probability of overlap is 72 percent for a 1-minute delay and 82 percent for a 2-minute delay. For rotations at 5-minute intervals, the probability of overlap is reduced to 32 percent, or to 50 percent for a 1-minute delay.
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23. D. L. Johnson, *Anim. Behav.* **15**, 487 (1967); ——— and A. M. Wenner, *ibid.* **14**, 261 (1966).
24. The colony was the gift of J. R. Tollet of Palo Cedro, Calif., who was suggested by H. H. Laidlaw of the University of California, Davis.
25. The colony was the gift of D. A. Grigg of Harper, Ore., who was suggested by W. P. Stephen of Oregon State University.
26. The queen in each colony had been originally obtained from H. E. Park of Palo Cedro, Calif.
27. The number tags were obtained from Chr. Graze K.G., Württemburg, Germany. Each set consists of numbers running from 0 to 99 in five colors, thus of 500 unique tags. By the addition of small dots of colored paint, the number of unique tags was increased to 2200.
28. N. E. Gary, personal communication.
29. The orange oil and peppermint oil were obtained from Safeway Stores, Inc., Oakland, Calif.
30. *Local Climatological Data August 1969; Local Climatological Data September 1969* (published by the U.S. Department of Commerce and available from U.S. Department of Commerce, Federal Building, Burns, Ore.).
31. Permission to use this site was kindly provided by J. W. Riley, district manager, Bureau of Land Management, Burns, Ore.
32. This information was provided by C. Bacon of the Bureau of Land Management, Burns, Ore.
33. The research discussed was funded by U.S. Public Health Service grant FR 07003 and by a grant from the Ford Foundation through the Associated Students of the California Institute of Technology Research Center. We thank Lynda MacLeod and Paul Carpenter for technical assistance, Dennis DiBartolomeo for technical assistance and aid in developing the capturing technique, Drs. N. E. Gary and H. H. Laidlaw for valuable technical advice, Dr. Ian Phillips for thoughtful criticisms, Dr. R. L. Sinsheimer for arranging much of the financial support, and especially Dr. Seymour Benzer, without whose interest, advice, and guidance the research would not have been possible.

A Scientific Safari to Africa

Africa needs help from U.S. scientists with its problems of health, agriculture, technology, and education.

Glenn T. Seaborg

As the technicians removed the sample containers from the target holder, the laboratory director explained how the radiation-attenuated organisms of the parasitic disease leishmaniasis were being tested to determine their immunological potential. Success would offer a means to control the vicious disease leishmaniasis, which disfigures and blinds millions in the tropics.

The scene I was witnessing and the explanation I was receiving were occurring not in a highly advanced U.S. medical research laboratory but on the outskirts of Addis Ababa, in a modest building that houses the Institute of Pathobiology of the Haile Selassie I University. The explanation of the application of one of the most advanced and progressive techniques for the control of parasitic diseases was being given by Aklilu Lemma, dean of the Faculty of Sciences of the university and director of the laboratory. I was visiting Ethiopia—and five other African countries—with several other U.S. scientists and scientific administrators (*1*) to become better acquainted with African science, to establish contacts between African and U.S. scientists, and to identify ways in which closer and more effective cooperation with science in Africa might be achieved.

In almost 9 years as chairman of the Atomic Energy Commission, I had already visited over 50 countries, ranging from the technologically and scientifically advanced nations of Europe to the developing states of Asia and Latin America. Despite my long-standing interest in Africa, I had avoided a visit there because I doubted whether the state of scientific—and especially of nuclear energy—development would justify the trip. Finally, however, conversations with other government officials led to the idea that a visit to Africa by a senior U.S. government science official would be beneficial. Secretary of State William P. Rogers gave the plan his enthusiastic support.

I was to visit Africa in my capacity as a scientist, rather than specifically as chairman of the Atomic Energy Commission. My purpose was to make a broad-ranging evaluation of science on that continent and of the prospects for beneficial scientific cooperation between the United States and the countries I would visit. An itinerary was drawn up which included six countries: Morocco, Tunisia, Ethiopia, Kenya, the Congo (Kinshasa), and Ghana. Both northern and sub-Sahara Africa and both English- and French-speaking areas were represented. A small group of outstanding scientists in the fields of medicine, biology, and agriculture was selected and was supplemented by appropriate government officials who could follow up any leads for increased cooperation.

Our group departed on 3 January 1970 and returned 13 days and 21,720 miles later. My predominant reaction on this trip was surprise—surprise that Africa had come as far as it has in science, in self-government, and in eagerness to move ahead. Although some of the countries we visited had only a handful of college graduates just 10 or so years ago, I returned with the conviction that, in many respects, Africa is moving faster (although from a more elementary base) and has more unclouded prospects for technological and economic progress than many developing nations in other parts of the world.

If the progress in Africa is surprisingly impressive, the needs are even more apparent. The efforts to develop a radiation-attenuated vaccine for the leishmaniasis organism is an example. In a well-equipped laboratory, the irradiation would be conducted with a small cobalt-60 gamma source, rather than with the electron accelerator with maximum energy of 300,000 electron volts that Dr. Lemma was using, in order to ensure uniformity of dosage throughout the entire sample. Dr. Lemma was well aware of this deficiency in his procedure and was anxious to correct it.

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