

SOUND PRODUCTION DURING THE WAGGLE DANCE OF THE HONEY BEE

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Introduction

The waggle dance of the honey bee appears to be a method by which the direction and distance of a food source is communicated among individuals. The direction in which the bee moves on the comb while wagging its abdomen has been interpreted (von Frisch, 1946, *et al.*) as the means by which the direction of the food-source is conveyed. Although good evidence exists that information is sent by this method (von Frisch & Lindauer, 1956), no direct evidence exists on how this information is received by other bees.

Von Frisch and co-workers found the time for a complete loop, time of wagging, and number of waggles to be equally good criteria for conveying distance information. These activities can produce either visual or tactile stimuli, although hive darkness and the observed intimate contact of dancing bees and other workers suggest the latter. Since chemicals diffuse rapidly, a chemical stimulus probably does not serve as a signal for distance of food sources.

The following study on the possible role of sound in communication developed after bees engaged in the waggle dance were found to produce an inaudible, pulsed sound while on the straight run part of the dance. Although the study of audible honey bee sounds has failed to establish that vibratory stimuli are important in the life of the colony (Frings & Frings, 1958), several distinct sounds are produced which are perceptible only through high amplification. Since the waggle dance appears to carry distance information as well as direction information, any sound produced during the dance could be the method of communication of distance information, particularly since the work of Hansson (1945), Lindauer & Kerr (1960), and Jarvis (1950) establishes that bees receive sounds transmitted through the substrate.

Methods and Materials

The study was conducted on the University of Michigan's Edwin S. George Reserve (Pinckney,

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Michigan) during the summer of 1959. The hives used were similar to the one-frame glass-sided observation hives which are commonly used for exhibits and classrooms; but the glass sides were held in place by one or two small nails placed in oversized holes and the four comb honey sections above the deep brood frame were replaced by a shallow frame.

Each colony was started by selecting one brood frame from a standard hive of Italian bees (*Apis mellifera ligustica* Spinola) and placing it with its accompanying bees in the observation hive. This frame was checked to insure that eggs were present. Each colony was then allowed to raise its own queen and increase its strength normally. During the recording, however, each of the two colonies used had its strength further increased by the addition of brood (when the station was at 100 m.) and of field bees (when the station was at 1050 m.). The additional strength increased the number of bees visiting the feeding station from 2-4 to 10-12 in each instance.

The hives were kept in a windowless enclosure (2 × 3 × 4 m.) at the end of a shed. Light leakage was enough to permit objects to be seen in the room once the eyes had become accustomed to the darkness. A flashlight headlamp was used to watch the movements of bees. This light did not disturb the bees but enabled the observer to see the actions of the bees and to read the marking code. Air movement through the shed was free. Checks throughout the summer disclosed no instance in which the room temperature (hive temperature during recording) differed by more than 2°F. from the outside temperature during recording. After leaving the entrance of the hive, the bees walked about 15 cm. before reaching an exit from the southeast side of the building.

The feeding station included an inverted jar of sugar syrup which was placed on a saucer with enough gap between jar and saucer to provide an automatic dispensing of the syrup into the saucer. The jar and saucer were placed on a box, raising the dispenser above the level of the weeds and grass. Syrup made by the following recipe was used to fill the jars each morning:

- 1 litre hot water
- 1 litre granulated sugar
- 10 drops peppermint flavouring.

Since evaporation occurred, the sugar concentration in the saucer increased and the strength of the peppermint odour decreased during each day.

Bees were trained to visit the station at increasing distances from the hive by a "leapfrog" method, using two stations about 10 m. apart. After one or more bees had visited the further station, the closer station was moved beyond it.

The feeding stations were moved about 200 m. through a wood, about 850 m. along a curving road in the wood, and the remaining 180 m. across a slightly rolling open area. Previous to each recording the two stations were moved to one place and enough time was allowed to insure that each bee had made at least one round trip at that distance.

Straight line distances from the hive to the feeding station were determined by map measurement. A map of the Reserve features was obtained by tracing from air photographs, the scale being determined from the distance between two U.S. Coast and Geodetic Survey section lines (1.6 km. apart).

When unwanted bees began visiting the station (indicated by a sudden increase in the number of unmarked bees at the station), the experimental hives were closed, all bees were killed which visited the station for the next 30 minutes, and the hives were reopened. Wasps (*Vespula* spp.) were netted during the day or trapped after the bees had stopped flying in the evening. Bumble bees (*Bombus affinis* Cresson) occasionally visited the station but did not present a problem.

The bees were individually marked while they fed on the syrup. A fine grass stem was dipped into thin model airplane enamel and the droplet was applied to the body of the bee. The thorax was coded as follows: The front left represented the number 1, the front right 2, the rear left 4, the rear right 7, and the centre 10. A spot on the abdomen represented 20. By using these marks individually and in combination, 39 different bees could be marked with the use of only one colour; and the number of each bee was instantaneously recognizable. A total of seven distinct colours were used.

When the stations were together at a desired distance from the hive and were being visited by marked bees, data were taken from these same bees while they danced in the hive. Dance sounds

were recorded at a tape speed of 15 inches per second by a high-fidelity tape recorder (Magne-mite 610-E) with an added pre-amplifier. An American Microphone Company D33A microphone was hand held within one cm. of the dancing bee while recording.

Although the surface of a brood frame is remarkably quiet, certain noises interfered with good recording. Airplanes produce a noise similar in frequency to dancing bees, disturbed bees produce a short burst of noise every 3-4 seconds, flying bees constantly produce noise, and ventilating bees may be active at any time. Placement of the hive a short distance from the outside entrance of the room forced bees to walk from hive entrance to outside entrance, eliminating most of the flight noise; free movement of air through the room kept the number of ventilating bees to a minimum. Although ventilating bees did not prevent the dance from being clearly heard, they did produce a noise on the tape which often prevented a good audiospectrograph from being made.

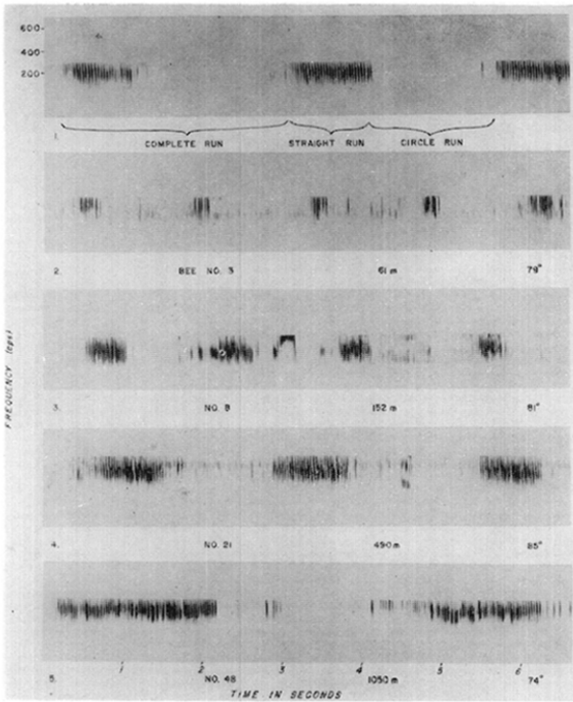
Notes taken between times of recording included any abnormal conditions noticed during the preceding recording period. Especially important events were recorded by voice. Sound produced during the straight run in the absence of abdominal wagging, lack of sound production while the bee was wagging, and collision of a dancing bee with another bee are examples of those notes which were taken while the tape recorder was running.

Most tape recording was done on mild days. However, some recordings were intentionally made on windy days for contrast. Wind direction was obtained from records of the University of Michigan Department of Meteorology at Ann Arbor, 40 km. to the southeast. Wind speed was calculated by use of a 3 m. high anemometer located on an open field on the Reserve, corrected by comparison with readings obtained at 15 m. in Ann Arbor to give an estimation of wind speed on the Reserve at a height of 15 m., the approximate height at which bees flew in the route used during this study.

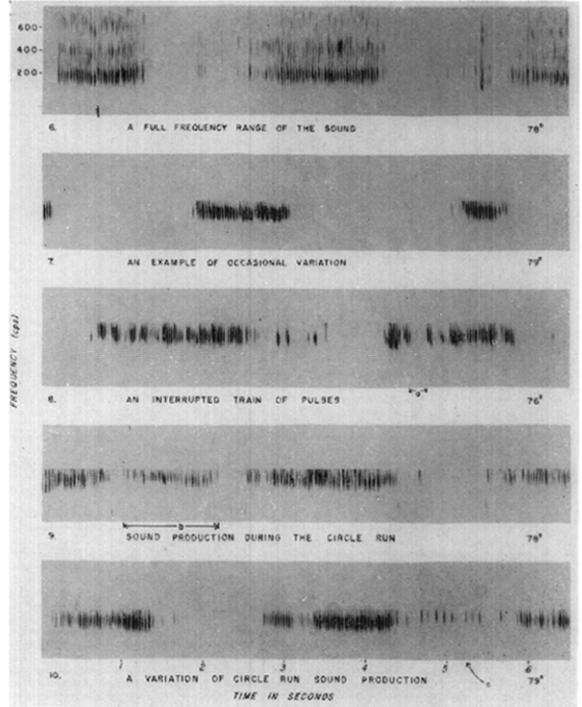
Temperature was read in the hive with a thermometer during the time of recording and outside by a recording thermohumidigraph at the Reserve weather station. All temperature readings given in this paper are those taken in the hive. Readings were taken on the floor of the hive beneath the brood frame.

To eliminate bias due to variations in machine speed, all audiospectrographs were made at one

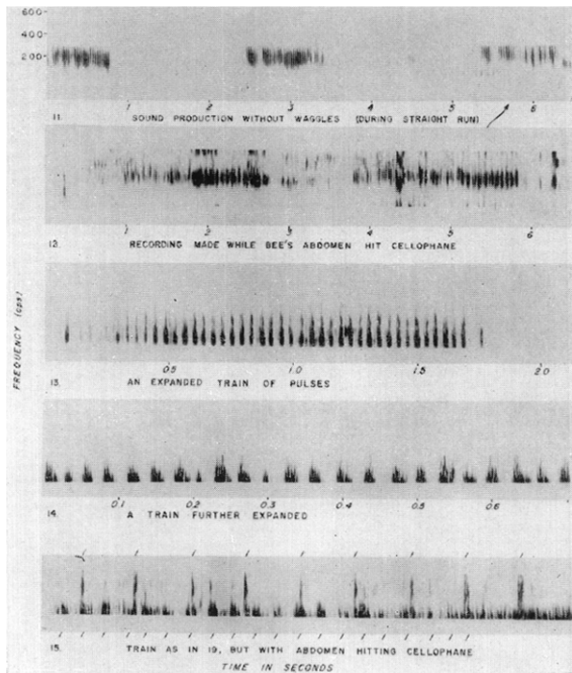
PLATE IX



Figs. 1-5.



Figs. 6-10.



Figs. 11-15.

time. Tapes were played on a Magnecorder PT 6A and the signal was fed into a Kay Electric Company Vibralyzer. After initial determination of the full frequency range of the sound (Plate IX, Fig. 6), all graphs were made without harmonics to save time. To eliminate personal bias, all audiospectrographs were coded and disarranged before measurement. Measurements were then made without a knowledge of the distance represented by each tracing.

In all audiospectrographs, time is represented on the abscissa, frequency on the ordinate, and relative intensities (within each graph) by darkness of the tracing. Since all dancing bees produce sound of approximately the same frequency (200 cps.), measurements were only made of time spent on each part of the dance and of the number of pulses produced during each straight run. Generally a dancing bee produced sound during the straight run and was silent during the circle run. Since the start and end of the sound production time was indefinite a somewhat arbitrary decision of the measurement of length of time spent producing sound was necessary. Darkness of pulses, configuration of total tracing, and relative length of tracings next to it in the series (by the same bee at the same time) were utilized in keeping this decision as consistent as possible.

Results

Description of the Sound

A labelled audiospectrograph (Plate IX, Fig. 1) illustrates the terms "straight run time," "circle run time," and "complete run time" as used in this paper (i.e. the time spent producing sound during the straight run, the silent period before the start of the next straight run, and the total of these two, respectively). The average of more than one "complete run time" must be identical with the average of more than one "Umlaufzeit" of von Frisch & Jander (1957), but experimentation must be done to establish the relationship between "Schwänzelzeit" (waggle time) and sound production time or between "Rücklaufzeit" (return run time) and the silent interval between straight runs.

The fundamental frequency of the straight run sound (essentially identical to the sound frequency of ventilating bees) is near 200 cps., with overtones at about 400 cps. and 600 cps. (Plate II, fig. 6). All other audiospectrographs shown include only the 200 cps. portion of the frequency range. Audiospectrographs of these signals compared to audiospectrographs of pure

tones confirmed these values. Since the frequency variation is so slight between recordings of different dancing bees that bee variance cannot be distinguished from machine variance, the frequency of the sound will not be considered further. ("Piping" bees, swarming bees, etc., produce sounds with the same fundamental frequency but with dominant overtones. These sounds are not discussed in this paper).

The sound is composed of pulses, examples of which can be seen in all audiospectrographs shown. The pulsed nature of the sound clearly separates this sound from audible sounds which are produced by workers (i.e. flight noise, ventilating hum, noises of disturbed bees, etc.). The straight run time is ordinarily made up of a continuous series of these pulses, the number of pulses dependent on the length of the straight run time. The "pulse rate" referred to in this paper is the number of these pulses produced per second. This rate was calculated by dividing the number of pulses counted by the length of time sound produced. "Pulse number" refers to the number of these pulses which are present in a straight run. The counting of this number was often difficult, and no counts were made in those trains of pulses where the pulses could not be separated or closely estimated.

Figs. 2-5 of Plate IX have been chosen only for their clarity as examples of bee dance sounds after these foragers had flown and collected syrup at various distances from the hive. Background noises blur some audiospectrographs (ventilating bees in Figs. 2 and 4 and a disturbed bee in the middle of Fig. 3). Ventilating bees provided the major source of interference in the audiospectrographs.

Although successive trains of sound were remarkably similar, extreme variation was occasionally present. Figs. 7 and 8 (Plate IX) show exceptional cases of variation in the straight run traces. Dancing bees were sometimes interrupted in their straight run when run into by another bee; at other times they apparently prematurely stopped their straight run for unknown reasons (Fig. 7). The measurements of these short runs were included in the computation of averages and standard deviations for each distance. However, bees interrupted during the straight run sometimes completed the straight run immediately after the disturbance had ceased (*a* in Fig. 8). In such cases measurements included both parts as one straight run.

In almost all tracings sound production was continuous during the entire straight run.

Occasionally sound was produced during the circle run, but this was easily discernible from the sound of the straight run. If the nature of the sound during the circle run was similar to that of the straight run, its intensity was usually much less (*b* in Plate IX, Fig. 9). Often sound produced during the circle run was of a different character (*c* in Plate IX, Fig. 10), being composed of discrete pulses rather than a continuous train of pulses. In either case the circle run sound could be more clearly separated from straight run sound by ear than by analyzing equipment. In all measurement of straight run sound production time, circle run sound was not included.

The Relation of Sound Pulses to Abdominal Wagging

At the beginning of the study sound produced during the straight run was believed to be produced by the wagging of the abdomen. Later, however, the following observations indicated that the sound was not directly produced by wagging: (1) An early analysis of a recording disclosed a pulse rate of about 35 per second, which was not similar to or an even multiple of von Frisch's 13 waggles per second. (2) Sound was sometimes produced when no wagging was visible (during the circle run—Plate IX, Figs. 9 & 10); and during the straight run—Plate IX, Fig. 11). (3) Wagging sometimes occurred when no sound could be heard. These latter two observations were repeated during the course of the study, although in most instances sound production and wagging were apparently coincident.

To compare waggle rate and sound pulse rate directly, a small bit of cellophane (about 2 mm. \times 1 cm.) was glued to the end of the microphone. The microphone was then held so the dancing bee's abdomen hit the cellophane. Two sounds were recorded simultaneously: the tapping of the abdomen against cellophane and the normal sound of the straight run. Although the two sounds could be clearly distinguished by ear, especially when the tape was played at slow speeds, the audiospectrograph was not clear enough for a comparison (Plate IX, Fig. 12). By expanding a train of pulses on the analyzing equipment (equivalent to slowing down the speed of tape while it is being played), however, it is sometimes possible to make a clearer audiospectrograph. For example, in Plate IX, Figs. 13 & 14 illustrate normal straight run traces which have been expanded. Fig. 15 of the same plate shows a train of pulses expanded as in Fig.

14, but with the sound of the tapping of the abdomen against cellophane also present.

Although the noise from the tapping of the abdomen against cellophane interferes with a clear appearance of the sound pulses, waggle rate and sound pulse rate can still be measured and compared. The marks placed on the bottom edge of Fig. 15 indicate the position of normal sound pulses; marks placed on the top edge of the figure indicate those times at which noise was produced by the bee hitting its abdomen against cellophane. By dividing the number of sound pulses (18) by the number of abdominal taps (7), a ratio of about 2.6 is obtained. If the average pulse rate of the sound produced by the bee during the straight run (31.1 per second) is divided by the average waggle rate (12.83 per second) from the study of von Frisch & Jander, a ratio of about 2.4 is obtained. In addition, a comparison of the average waggle rate of 6 different bees in this present study to the average pulse rate of 3 of these bees yields a ratio near 2.3. From these calculations, the ratio of the rate of sound pulse production to the rate of double wagging is evidently near 2.5. Clearly the wagging and sound pulses are not produced by the same muscular activity.

Summary of the Data

Table I contains a summary of the data obtained during the study. The distances given at the left are for all of the distances at which bees flew to visit a feeding station before they were recorded in the hive. The bee numbers (a different number for each different bee) indicate the total number of different bees recorded as well as those instances in which the same bee was recorded at different distances. If the same bee was recorded two or more times at the same distance, the data given for that bee is a weighted average.

The complete run times, straight run times and circle run times in seconds are preceded by the number of runs upon which each is based. To eliminate some of the effect of small sample error, all of the times for which the number of runs on the straight run was less than five are included in the table but were not used for calculations of means and are not shown on the graphs. These values are marked with an asterisk (*).

The number of runs from which the pulse rate is determined is lower than that given in the three preceding columns. This lower number is a result of the difficulty of accurately determining

Table I. Summary of the Data.

distance and bee no.	complete run time		straight run time		circle run time		pulse rate (corrected)				temp. F°	wind		
	no. of runs	ave. time	no. of runs	ve. time	no. of runs	ave. time	no. of runs	ave. no. of pulses	pulses per sec.	pulses per sec.		speed m/sec.	dir. (out)	
31m. 1	26	1-41	28	0-34	26	1-07	19	11-3	34-8	33-2	77	3-0	150°	
61	1	37	1-56	39	0-33	37	1-23	28	12-0	33-0	31-7	80	4-5	75°
	2	9	1-87	10	0-14	9	1-73	7	5-9	37-4	34-2	80	1-4	75°
	3	33	1-44	35	0-15	33	1-29	28	5-0	34-9	31-6	79	4-5	90°
	4	40	1-58	41	0-30	40	1-28	38	8-9	30-0	28-6	79	1-4	90°
100	10	15	1-44	16	0-32	15	1-12	5	10-8	35-4	33-7	86	2-2	80°
	11	45	1-72	50	0-18	45	1-54	26	5-5	31-5	29-0	86	2-2	80°
	12	5	1-63	6	0-38	5	1-25	4	13-2	35-0	33-6	73	2-8	10°
106	1	46	1-86	52	0-31	46	1-55	37	9-8	30-0	28-7	80	1-4	75°
	5	27	1-51	29	0-28	27	1-23	18	10-2	34-2	32-6	78	4-5	75°
	3	13	1-89	14	0-23	13	1-67	7	6-0	31-3	29-0	80	4-0	0°
	6	12	1-53	13	0-14	12	1-39	10	5-4	39-0	35-2	80	1-4	0°
	7	2	1-62*	3	0-18*	2	1-47*	3	6-3	35-1	32-4	80		
152	8	19	1-99	23	0-45	19	1-52	18	15-3	36-4	35-1	81	2-5	135°
	9	15	1-77	17	0-30	15	1-47	14	9-7	32-2	30-7	81	2-5	135°
192	13	59	1-93	60	0-82	59	1-11	14	28-6	36-8	36-1	83	3-7	70°
	14	0	1	0-72*	0	—				83	3-7	70°
295	15	30	2-40	35	0-56	30	1-84	25	16-6	32-3	31-4	81	3-0	175°
	16	16	2-18	20	0-49	16	1-69	13	15-5	31-1	30-2	81	3-0	175°
	17	21	2-10	24	0-71	21	1-38	3	27-3	39-1	38-2	81	2-8	175°
	18	11	2-04	13	0-52	11	1-53	6	19-3	35-8	34-8	81	2-8	175°
	19	29	2-18	31	0-55	29	1-62	4	21-8	37-7	36-7	81	3-4	175°
490	20	8	3-09	10	0-74	8	2-34	10	25-7	34-6	33-9	85	1-0	95°
	21	35	2-57	39	0-86	35	1-71	32	25-6	29-7	29-2	85	0-9	95°
	22	42	2-32	43	0-90	42	1-41	29	24-7	27-2	26-8	85	0-7	95°
	23	8	3-26	8	1-00	9	2-21	5	33-4	32-8	32-3	78	2-3	65°
	24	27	2-86	29	1-45	27	1-41	26	39-0	26-9	26-6	78	2-3	65°
700	25	30	2-96	31	1-27	20	1-69	25	34-6	27-2	26-9	79	0-5	125°
	26	5	3-60	6	1-01	5	2-50	6	30-8	30-5	30-2	79	0-5	125°
	27	28	3-42	31	1-20	28	2-19	24	33-1	28-2	27-9	79	0-8	125°
	14	6	2-82	8	1-05	7	1-77	4	36-5	34-1	33-6	79	0-8	125°
	28	10	2-61	11	1-02	10	1-59	11	31-0	30-5	30-0	79	1-2	125°
	29	4	2-58	6	1-27	4	1-21	—					1-4	125°
	30	15	2-96	18	0-94	15	2-02	18	32-8	34-9	34-3	79	0-9	125°
	31	6	2-86	7	1-40	6	1-46	5	43-6	30-0	29-7	79	0-9	125°
880	24	26	3-46	27	1-53	26	1-93	14	42-0	25-3	25-1	78	2-4	140°
	32	16	4-13	18	1-68	18	2-38	12	46-3	28-4	28-1	78	2-0	140°
	33	13	3-69	16	1-47	13	2-19	12	42-8	29-7	29-4	78	2-2	140°
	34	1	3-85*	2	1-56*	1	2-64*	—					1-8	140°
	35	0	1	1-34*	0	—					1-8	140°
	36	10	3-49	11	1-07	10	2-45	8	30-0	27-6	27-2	78	1-8	140°
	37	4	3-84	5	0-95	4	2-84	—					1-8	140°
	38	2	5-91*	3	1-28*	2	4-74*	3	37-0	30-7	30-3	78	1-8	140°
	39	4	3-42	5	1-31	4	2-17	5	34-4	26-2	25-9	78	1-8	140°
	23	7	3-15	8	1-30	7	1-85	7	39-3	29-9	29-6	78	1-5	55°
	40	8	3-61	10	1-30	8	2-30	9	38-1	28-6	28-3	78	1-2	55°
1030	41	16	3-66	16	1-65	17	2-06	—					2-1	45°
	23	12	3-07	13	1-38	12	1-69	12	38-8	28-2	27-9	83	2-1	45°
	38	4	4-56	6	1-62	4	2-95	4	48-8	30-2	29-9	83	1-8	45°
	42	9	4-00	10	1-75	9	2-24	7	59-6	33-8	33-4	83	1-8	45°
	43	9	4-18	10	1-93	9	2-26	—					1-8	45°
	40	4	4-10	6	1-72	3	2-46	5	55-4	31-0	30-7	83	2-5	45°
	28	3	3-78*	3	2-87*	4	1-59*	—					1-8	45°
34	8	3-71	9	1-31	8	2-40	3	38-0	27-9	27-6	83	1-8	45°	

Table I. Summary of the Data (continued).

distance and bee no.	complete run time		straight run time		circle run time		pulse rate ave. (corrected)				temps. °F	wind		
	no. of runs	ave. time	no. of runs	ave. time	no. of runs	ave. time	no. of runs	no. of pulses	pulses per sec.	pulses per sec.		speed m/sec.	dir. (out)	
1050	41	22	3.81	24	1.65	22	2.16	8	50.5	29.5	29.3	80	2.2	45°
	28	20	4.22	22	1.82	20	2.41	—	—	—	—	—	2.5	40°
	44	22	3.98	24	1.84	22	2.03	7	60.3	32.8	32.6	74	1.0	40°
	45	8	3.71	9	2.50	10	1.28	—	—	—	—	—	1.4	15°
	46	19	3.80	20	1.36	18	2.38	10	46.0	34.4	34.0	74	1.0	40°
	47	1	3.70*	2	1.11*	1	2.71*	—	—	—	—	—	0.7	40°
	48	13	3.95	15	2.18	13	1.75	5	69.0	34.1	33.9	74	0.3	40°
	49	4	3.63	5	1.68	4	2.05	—	—	—	—	—	0.3	40°
1100	28	8	3.67	11	1.81	8	1.91	—	—	—	—	—	1.5	0°
	50	3	4.02*	4	2.90*	3	1.33*	—	—	—	—	—	1.4	0°
	51	12	3.78	13	2.29	12	1.47	—	—	—	—	—	1.1	0°
	52	5	3.52	7	1.68	5	1.83	4	53.8	32.0	31.7	80	1.1	0°
	53	6	3.78	6	1.80	6	1.96	—	—	—	—	—	0.3	0°
1120	65	15	3.16	17	1.26	15	1.89	7	44.0	33.2	32.8	74	4.2	120°
	60	7	3.65	9	1.55	8	2.16	5	49.0	30.1	29.8	74	4.2	120°
1158	49	5	4.35	6	1.97	5	2.41	—	—	—	—	—	1.1	60°
	51	10	4.05	11	2.14	11	1.96	—	—	—	—	—	1.1	60°
1230	54	13	3.30	14	1.55	13	1.75	—	—	—	—	—	4.2	90°
	55	18	4.13	22	2.32	19	1.85	—	—	—	—	—	4.0	70°
	50	21	4.40	22	2.61	21	1.82	—	—	—	—	—	4.5	80°
	28	18	4.20	22	2.05	18	2.14	4	60.2	28.4	28.2	85	4.0	70°
	56	3	4.14*	4	2.30*	3	1.88*	—	—	—	—	—	4.2	70°
	46	10	3.87	14	1.93	11	1.86	8	63.6	32.4	32.2	—	3.5	80°
	57	4	3.47	5	1.83	4	1.70	—	—	—	—	—	2.1	60°
	58	7	3.34	8	2.02	7	1.36	—	—	—	—	—	2.8	60°
	23	2	3.87*	3	1.87*	2	1.87*	—	—	—	—	—	2.8	60°
	59	12	3.41	13	1.70	12	1.71	5	57.2	31.6	31.4	76	2.8	60°
	60	11	3.64	12	1.95	11	1.69	7	69.6	34.8	34.5	76	2.8	60°
	61	8	3.96	9	2.07	9	1.79	4	63.2	32.5	32.2	76	2.5	60°
	62	1	3.48*	2	2.28*	1	1.02*	—	—	—	—	—	4.2	90°
	63	2	3.70*	3	1.95*	2	1.82*	—	—	—	—	—	4.2	90°
	64	2	4.66*	3	2.48*	2	2.13*	—	—	—	—	—	4.2	90°

the number of pulses for the entire straight run. To eliminate some of the effect of small sample error, those values which are based on less than three runs are not included in the table and are not shown on the graphs or used in calculation.

The average number of pulses is a weighted average. The pulse rate is not computed by dividing this number by the straight run time given in the table but by dividing this number by the average time spent on those straight runs which were clear enough for pulses to be counted. The pulse rate given in the table, therefore, cannot be exactly derived from the straight run time and the number of pulses given in the table.

The wind speed listed is an average of the recorded wind speeds for the 15 minute period before the sound of the dancing bee was recorded. The "wind direction" represents the

direction of the wind with respect to the bee on its outward flight (i.e. 0° means the bee was heading directly into the wind, while 45° means the bee was heading into a wind which was either right or left of the line of flight of the bee). Both wind speed and direction varied so much even within five minute periods that these figures must be considered approximations.

Graphs of the Data

Figs. 1-4 present the data of Table I graphically. Figs. 1 (a & b) and 2 illustrate the relationship of the average complete run times, straight run times, and circle run times to the distance of the feeding station from the hive. The line through the points of Fig. 1b was fitted by the method of least squares ($y=0.15+0.069x$). The lines through the points of Fig. 1a

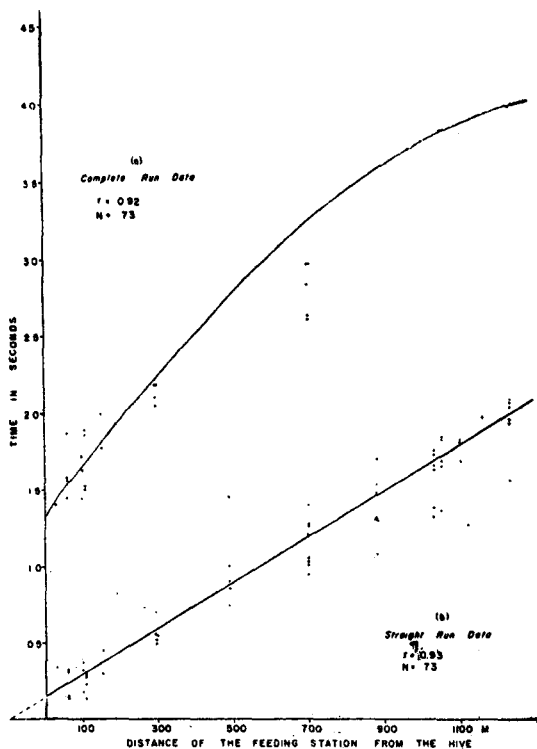


Fig. 1. Average complete run times and average straight run times for dancing bees which had visited feeding stations at various distances from the hive.

and Fig. 2 were fitted by sight. The positions of these latter two lines were adjusted to best fit the points and yet have the sum of the straight run line and the circle run line exactly equal the total run line. The lines through the complete run and circle run data do not differ significantly from those given by von Frisch & Jander. The line through the straight run data of this study, however, differs from the line of von Frisch & Jander in being straight rather than convex, at least over the distance covered by this study. Further experimentation would be necessary to determine if this straight line relationship would hold when the feeding station was placed at greater distances from the hive.

In a comparison of the complete run time, straight run time, and circle run time, the high correlation of the straight run time data (0.93), the simplicity of the line and the low intercept of the line make this element of the dance the most likely transmitter of the distance information. The line through the straight run time data intercepts the abscissa at about -100 m. If the

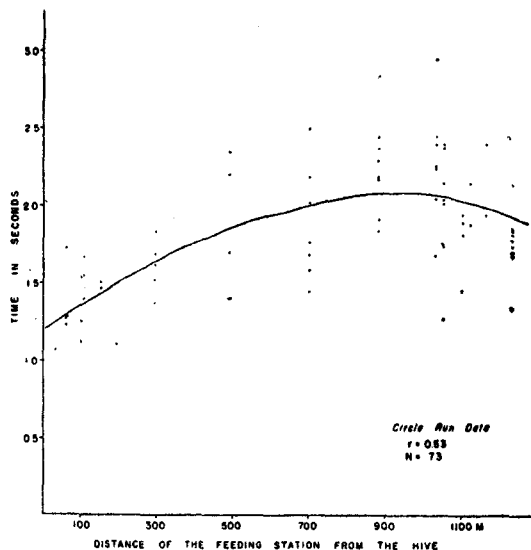


Fig. 2. Average circle run times for dancing bees which had visited feeding stations at various distances from the hive.

intercept had been at 0 m., a direct conversion from the time spent on the straight run to the time spent in flight would have been suggested. Such a relationship may still hold, however, if this offset represents time needed to reach flying speed, time spent circling before landing, or the total of the two. This constant would be the same regardless of the feeding station distance. According to the results of this study, this discrepancy in time cannot be considered an effect of wind speed or direction.

The graph of the circle run time (Fig. 2) has a slight rise in the middle which does not appear to be related to any of the environmental factors measured. The significant correlation of the time of this element with distance (0.53) indicates either that some message is conveyed by the circle run time or that a longer straight run time results in a longer circling time. (Heran, 1956, found that dancing bees travel somewhat further on the comb when dancing after visiting further stations than after visiting closer stations).

Since the lines of Figs. 1 and 2 were fitted to complement each other, the curve in the line through the circle run data must be reflected in the line drawn through the data for the complete run time; Fig. 1a illustrates this effect. The high correlation of the complete run time with distance (0.92) indicates either that the complete run time transmits the distance information or

that the complete run time correlation is merely a reflection of the high correlation of the straight run time.

Full logarithmic plots of the data for the straight run times, circle run times and complete run times were made. These graphs do not clarify the relationships and are not included in this paper.

Pulse rate would normally be expected to increase with an increase in temperature, but the data obtained in this study fail to support this view (correlation -0.08).

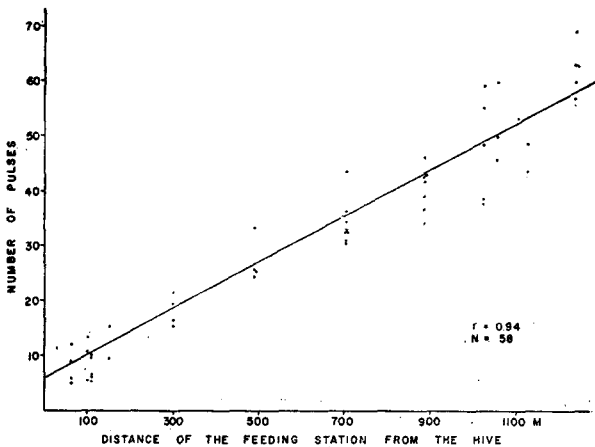


Fig. 3. Average number of pulses during the straight run for dancing bees which had visited feeding stations at various distances from the hive.

Pulse number plotted against distance of the feeding station (Fig. 3) shows a relationship similar to that obtained for the graph of the time spent on the straight run. The major difference lies in the sigmoid configuration of the points, a configuration which is barely noticeable in the data for the straight run time. The coefficient of correlation of the pulse number-distance relationship (0.94) is not significantly different from that obtained for the straight run time-distance relationship (0.93). Since the regression lines are similar (in Fig. 3, $y=6.0+0.425x$) and the correlations of these elements with distance are nearly identical, a direct comparison between these two elements is shown in Fig. 4, in which the average values for the straight run time and pulse number for any one bee at any one distance have been plotted against each other. The coefficient of correlation (0.98) establishes that, on the basis of the available

data, the two elements cannot be separated. Therefore, the straight run time and the number of pulses per straight run will be considered interchangeable throughout the remainder of the paper.

Pulse Rate Correction

The number of pulses in a train is the number of dark vertical bands; the length of time sound is produced is measured from the beginning of the first band to the end of the last. The ratio of these two numbers, however, is a biased estimate of the pulse rate, since a full pulse cycle includes not only a dark band but also the following light region. Thus, the ratio of pulse number and straight run time as measured in this study over-estimates the true pulse rate, the degree of over-estimation being inversely related to the number of pulses in the train. Correction of the pulse rate requires an estimate of the width of the space between pulses on the audiospectrographs.

An expanded train of pulses shows a clear relationship between the width of a pulse and width of the following space. In Plate IX, Fig. 14 illustrates that 22.5 pulse cycles were produced during 0.7 seconds. The ratio of the average width of these dark bands to the average width of the space between bands is 1.23. Computation from these measurements yields 0.014 seconds for the average width of a space between pulses. If the ratio of dark bands to light spaces (1.23) is applied to data selected by chance from

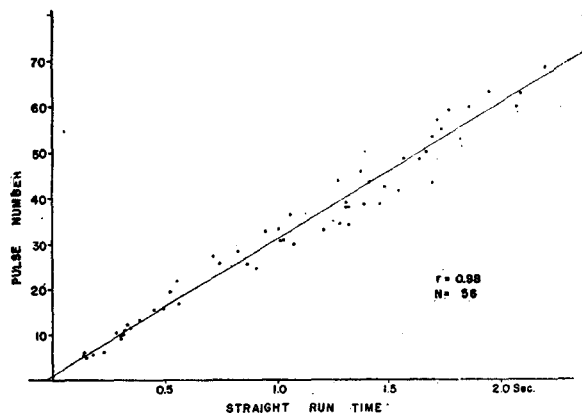


Fig. 4. The average number of pulses during the straight run compared to the average time spent on the straight run.

each of several distances, by using the formula $b = \frac{T}{2.3N - R}$, where T = total time for all runs, N = total number of pulses and R = number of runs, an average time of 0.015 seconds is obtained for the time between pulses (b), a value similar to that obtained from the expanded train. The derived values varied only slightly.

An average width of the space between pulses can also be estimated from the data included in Fig. 4. The regression line shown ($y = 0.836 + 30.54x$) intercepts the abscissa at -0.027 rather than at the origin, while the regression line not shown intercepts the origin at $+0.003$ —the true intercept is near the difference between these two values. An average between these two values is identical to the value of 0.015 seconds obtained above.

The following formula, which will give an approximate value for the corrected pulse rate for each bee for each distance, can now be derived:

$$\text{corrected pulse rate} = \frac{(\text{pulse number})(\text{pulse rate})}{(\text{pulse number}) + (0.015)(\text{pulse rate})}$$

The values for these corrected pulse rates are given in the designated column of Table I.

Analysis and Discussion of the Results

Introduction

The graphs of the results (Figs. 1-3) suggest that complete run time, straight run time, and number of pulses are equally accurate carriers of information concerning the distances of the feeding station from the hive. A more detailed analysis of the data may reveal small differences which favour one of these possibilities. von Frisch & Jander were not able to establish which part of the dance transmitted the distance information; among the five elements they considered, complete run time, straight run waggle time or number of waggles were most closely related to distance. Although they chose the straight run time as the probable transmitter of distance information, they concluded that complete run time and number of waggles could not be discarded as possibilities. Unfortunately, since no experiments have been done to determine whether or not the period of sound production during the straight run is coincident in time with wagging of the abdomen, results of this present study cannot be directly compared with the results of the study of von Frisch & Jander, an exception being the complete run time averages. If, however, complete run time can be eliminated as a signal for distance of the food source by

results of this study, the same conclusion will probably hold true for the complete run time in the study of von Frisch & Jander. In a consideration of the significance of different components, the significant correlation of the circle run time with distance of the feeding station from the hive (0.53) cannot be disregarded.

Analysis of Variation

The data for complete run time, straight run time and circle run time can be subjected to an analysis of variation. This analysis should clarify the relationship among these three components of the dance by establishing how much of the variation at a given distance is a result of variation within bees and how much is a result of variation between bees. These variations can then be compared to each other.

The usual work form for variance analysis was modified to accommodate occasional extreme values that occur in behaviour data. Such values distort variance estimates and are not expected in the model of a normal distribution; yet the process of discarding them may introduce subjective conclusions. Hence, where variances of individual measures were computed, the 8-point percentile method was used (Dixon & Massey, 1951), a method which ignores the numerical value of numbers outside the 3-97 percentile range. The efficiency of this method as a substitute for the usual formula for variance is high (0.86). The following work form was used:

Source of estimate	n		Variance
between means	$K - 1$	$N_i(\bar{y}_i - \bar{y}_T)^2$	s_g^2
within bees	$N - K$	8-point percentile method	s_p^2
total variance	$N - 1$	8-point percentile method	s_T^2

K = total number of bees.

N = total number of observations.

N_i = number of observations for an individual bee.

\bar{y}_i = mean for an individual bee.

\bar{y}_T = mean for one distance.

$F = s_g^2/s_p^2$

In the analysis only those distances were considered for which there were four or more bees and only those bees were considered for which there were five or more straight runs.

The within-bee variance (s_p^2) for each distance was computed directly from raw data by placing the data for each bee on a separate frequency distribution, aligning medians of the different distributions to a common point, and calculating variance by the 8-point percentile method.

The total variance at each distance was also computed from raw data by the 8-point percentile method after the measurements of the performance of all bees had been placed on a common frequency distribution, without aligning medians. A comparison of this method with the usual method of computing standard deviation showed a negligible difference in results when applied to those samples which lacked extreme values.

Table II. Variation Analysis Values of F.

Distance	Complete Run	Straight Run	Circle run
61 m	2.7*	32.0**	4.2**
106	7.4**	15.2**	5.7**
295	2.6*	7.7**	6.9**
490	40.6**	226.0**	32.3**
700	6.6**	10.0**	7.6**
880	2.1	9.6**	1.8*
1030	6.2**	17.4**	4.7**
1050	1.1	22.0**	4.5**
1100	0.3	10.1**	3.3*
1230	14.3**	26.6**	2.2*

The values of F (s_g^2/s_p^2), given in Table II, are followed by asterisks denoting the 5 per cent. (*) and 1 per cent. (**) levels of significance. Of the three elements subjected to analysis, the straight run time is the most consistent as to the level of significance of the F value, but in general, one must conclude that real differences between bees exist in all three dance components.

Estimates of the amount of variation between bees (assuming samples of infinite size, thereby eliminating sampling error of the within-bees component) can be obtained in the following way (Snedecor, 1946):

$$s_b^2 = \frac{s_g^2 - s_p^2}{k}$$

$$\text{where } k = \frac{1}{K-1} \left(N - \frac{N_i}{N} \right)^2$$

In this way, total variance is partitioned into between-bees and within-bees components. The corresponding standard deviations are graphed in Figs. 5 b-d.

The standard deviations (measured in seconds) obtained in this study (Fig. 5b) are not markedly different from the corresponding standard deviations obtained by von Frisch & Jander (Fig. 5a). The separation of the straight run time standard deviations from standard deviations of the complete run time and circle run time as seen in Fig. 5b, however, is present to a greater extent than in the results of von Frisch & Jander. This difference between the two studies may prove to be only a result of the different accuracy with which sound production or waggle time can be measured.

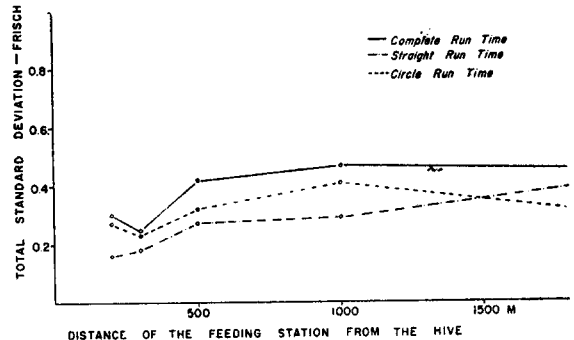


Fig. 5(a). The total standard deviations in seconds from the work of von Frisch compared to the distance of the feeding station from the hive. Only those distances are represented which correspond to the distances covered by this present study.

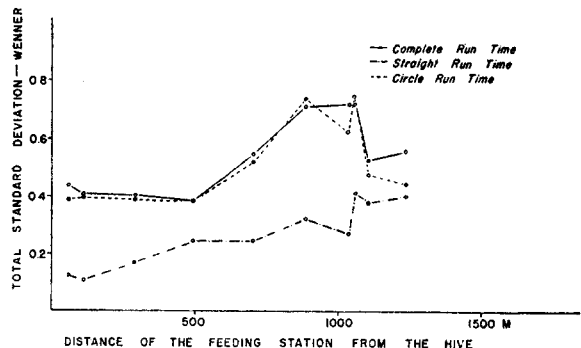


Fig. 5(b). The total standard deviations in seconds from this present study compared to the distance of the feeding station from the hive.

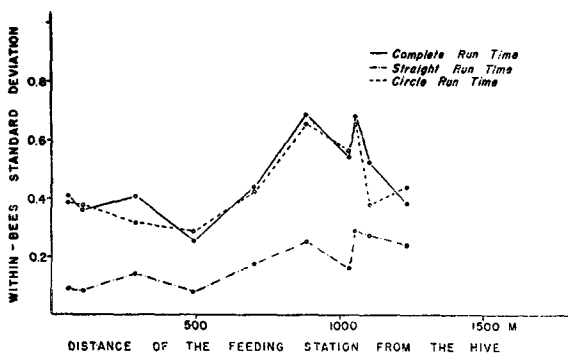


Fig. 5(c). The within-bees standard deviations in seconds compared to the distance of the feeding station from the hive.

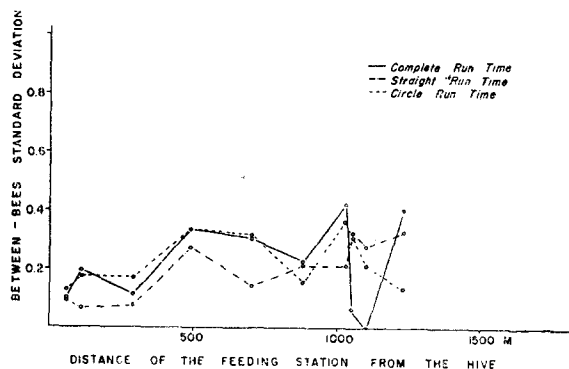


Fig. 5(d). The between-bees standard deviations in seconds compared to the distance of the feeding station from the hive.

A comparison of Figs. 5 b-d shows that the within-bees component is responsible for the pattern of the total variance and that the complete run time variance evidently reflects the circle run time variance. From Fig. 5c one can also see that bees are performing the straight run with more precision than the circle run or total parts of the dance.

That variance which cannot be eliminated by averaging (if a receiving bee could average) is illustrated in Fig. 5d. This between-bees variance, the error of converting distance flown into a signal which can be used by other bees, can be seen to be present equally in all components of the dance, and remains in the system if receiving bees average an infinite number of runs by the sender.

The within-bees variance, on the other hand, is reduced by averaging, the remaining amount

being inversely proportional to the number of runs averaged.

The following formula, therefore, gives the total variance in the average performance of an individual:

$$s_T^2 = \frac{s_p^2}{N} + s_b^2$$

Since within-bees variance of the straight run is nearly equal to between-bees variance, whenever four or more runs are averaged, the remaining variance is due largely to that between bees and is of about the same magnitude whether ten or fifty runs are averaged. Hence, in the preceding analysis, averages for bees were weighted equally (one point each on the graphs), independent of sample size. Although a slight error in analysis exists, a greater error would be introduced by using weighted means.

In the other two dance components, within-bees variance exceeds between-bees variance, so that its contribution to total variance becomes small only at a sample size of ten or more observations. For these components, therefore, the error in analysis that results from equal weighting of means is greater than that in the analysis of straight run data, although it is still less than the error that would result in the use of weighted means.

Comparisons of Deviations

There is an alternative method of comparing the total errors of each of the dance components. Averages were computed for those runs of a single bee at a given distance which were recorded within an hour, provided four or more records were available. If one bee made one or more trips to the feeding station between the times its dance sounds were recorded, each set was averaged separately. A total mean was then computed for each of these times at each distance, and deviations from these means were tallied.

The high correlation (0.61) between deviations for complete run time and circle run time confirms the idea gained from the analysis of variation that variation of the complete run time reflects variation of the circle run time. The correlation of 0.43 between deviations for complete run time and straight run time indicates that the complete run variation also reflects variation present in the straight run time. This strong evidence, which suggests that the average complete run time is a total of the averages of the other two components is offset, however, by the negative correlation (-0.34) between

deviations from the mean of the straight run time and circle run time. This inverse correlation shows that bees which spend a greater than average time on the straight run tend to spend a shorter than average time on the circle run and vice versa, a relation that is not expected on the basis of earlier analyses in this paper.

Two facts are now evident: (1) The circle run time shows a positive correlation with the distance of the feeding station from the hive; and (2) Circle run time varies inversely with straight run time. These two observations are not, as might appear at first sight, mutually contradictory because the former is concerned with variations between distances whereas the latter refers to variations within distances.

Bee number 28 flew six different times at four different distances, and the values of its deviations were found to be more or less evenly distributed among the values for other bees. Therefore, a single bee is probably not consistently biased, and that variation ascribed to "between bees" actually occurs "between occasions."

Effects of Wind Direction

The graphs of the data (Figs. 1-3) and of the results of the analysis of variation (Figs. 5 b-d), coupled with a comparison of the coefficients of correlation, indicate that the straight run time is a better choice as a transmitter of distance information than either complete run time or circle run time. One environmental factor, wind, if it affects the dance, should most affect that element of the dance which transmits information about the distance of the food source. A study of the effects of wind upon the dance should then either support or contradict the conclusions previously reached in this paper.

A successful forager may pick up an estimate of the distance flown by any one or more of at least three methods (von Frisch & Lindauer, 1956): (1) energy used in travelling the distance; (2) actual ground distance flown; and (3) time spent in flying. If a bee converts the ground distance flown into a signal (2), wind speed and direction should not affect the signal. If a bee converts the energy used in travelling (1) or the time spent in flying (3) into a signal (these two concepts may prove to be inseparable), either the outgoing or incoming trip could be the period of time when the distance information was gathered. The manner in which wind affects or fails to affect different dance elements should clarify

the relationship of these dance elements to each other.

Since wind measurements were only approximate, a simplified analysis was designed. The data was separated into two components, data from those bees which generally flew against the wind on the way to the feeding station (0° - 75°), and data from those bees which generally flew with the wind on the way to the feeding station (120° - 180°). Side winds (76° - 119°) were disregarded. Each point of Figs. 1-3 was then evaluated as to the amount and direction of its vertical deviation from the regression line and classified according to the direction of wind in relation to the bee's outward flight (Fig. 6).

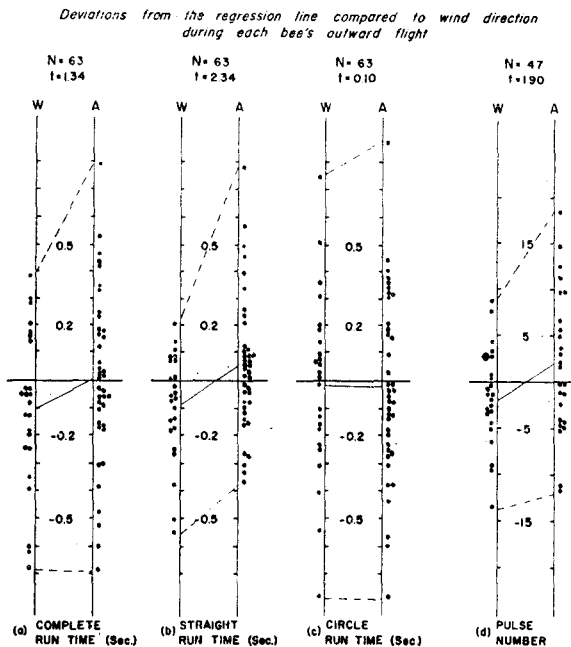


Fig. 6. The effect of wind direction on the various elements of the dance. Data on each element has been separated into two components; (W) for the data on those bees which flew with the wind on the way to the feeding station, and (A) for the data on those bees which flew against the wind on the way to the feeding station. Each point on the chart represents the amount and direction of the vertical deviation from the regression line for one of the points in Figs. 1, 2, or 3. The solid horizontal line represents the position of the regression line, the solid diagonal line connects the means, and the broken lines connect the extremes.

In Fig. 6a values obtained from the above procedure have been separated into two columns: W heads the column of those points

obtained when bees flew with the wind and *A* heads the column of those points obtained when bees flew against the wind. The horizontal line connecting the two columns represents the position of the regression line through the data of Fig. 1*a*; points have then been placed above or below this horizontal line a distance equal to the amount they were above or below the regression line of Fig. 1*a*. A solid diagonal line connects the observed mean of each column; broken lines connect extremes. Figs. 6*b* & *c* illustrate the results when this procedure was applied to data of the straight run time and circle run time. The data for the number of pulses was also subjected to this analysis (as a further check on the relationship between it and straight run time) by placing it on a similar, but not identical, scale (30 pulses=about 1 second) to that of the other three figures.

The equal number of points ($N=63$) in Figs. 6*a*, *b*, and *c* allows a direct comparison of results for the complete run time, straight run time, and circle run time. Of these three elements, the straight run time is the most affected by wind directions; bees which flew with the wind on the way to the feeding station generally indicated a shorter distance than would be expected on the basis of the location of the regression line through all the data ($t=2.34$, $p=\sim 0.02$). The complete run time reflects this variability due to wind, a further indication that the good correlation of complete run time with distance of the food source from the hive is simply a result of its straight run time component. The circle run time exhibits an insignificant degree of variation due to wind ($t=0.10$), indicating that this element of the dance does not carry information that is affected by wind.

The configuration of the pulse number Fig. 6*d* is very similar to that of the straight run time figure (6*b*). Since the number of points on which each is based is different ($N=63$ for straight run time, 47 for pulse number), and since the value of t increases with sample size, the differences in the values of t (2.34 for straight run time, 1.90 for pulse number) for these two elements can be shown to be insignificant. The effect of wind confirms that straight run time and pulse number are inseparable.

Another result of the wind direction (Fig. 6) is that the slope of the line between the means is positive. Since the direction of the wind given in this study is the direction with respect to the bee on its outward flight, this positive slope indicates that bees probably obtain their in-

formation about the distance of the food source on their outward flight. This conclusion was reached by von Frisch (1948) when he compared the number of runs executed per quarter minute to the distance of the feeding station. His data on wind effect on the complete run time showed the same effect as that obtained in this present study. More recently, Shaposhnikova (1958) conducted a series of experiments which involved moving the feeding station during the experiment. His results indicate that bees obtain their information about both the distance and direction of the food source on their outward flight.

Analysis of von Frisch's Step-experiments

Von Frisch and his co-workers conducted step-experiments ("Stufenversuchen") several times at several distances in attempts to measure performance of bees responding to the dance signals given by successful foragers (von Frisch & Jander, 1957). In these experiments bees were trained to visit a feeding station at a particular distance, marked, and allowed to return to the hive. These foraging bees thereupon danced, alerting other bees to the location of the food source. Before recruited bees left the hive, however, scent posts (with no food) had been placed in a direct line with the feeding station but at various distances from the hive. As recruited, unmarked bees left the hive in response to the signal given by the dance, they arrived at one of the scent posts and were then counted by an observer. Those newly recruited bees which arrived at the feeding station were counted and killed but were not included in the graphs or calculations of von Frisch & Jander.

The results from the step-experiment which had a feeding station at 750 m. from the hive are shown in Fig. 7*a*. This figure differs from that given by von Frisch & Jander by inclusion of the data for those bees which arrived at the feeding station (von Frisch, 1952) as well as for those bees which visited scent posts (since unmarked bees arriving at the feeding station presumably respond to the dance signal as much as unmarked bees arriving at the scent posts). Using data from this step-experiment and from other step-experiments (excluding those unmarked bees which were killed at the feeding station), von Frisch & Jander computed standard deviations and compared this error of field bee performance with the distance error they found indicated by the dance. In their comparison they found less error in the performance

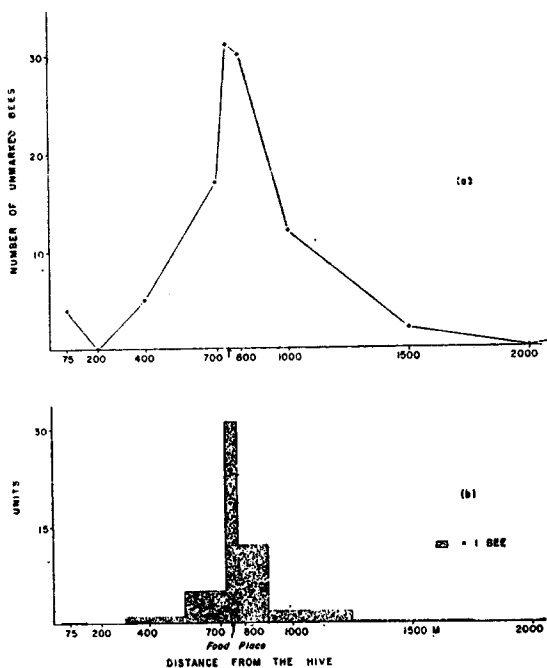


Fig. 7. Two methods of illustrating the results of bee performance obtained from von Frisch's step-experiments ("Stufenversuchen"). A line graph including all of the data is shown in (a); the same results in the form of a bar graph are shown in (b).

of recruited bees than was present in the performance of the dance by foraging bees. Since this is contrary to what one would expect—error of the signal given by the dance coupled with error of performance by recruited bees should add to give the expected error of field bee performance—von Frisch & Jander concluded that receiving bees probably averaged information from several runs and thereby obtained a more accurate estimation of the distance to be flown than could be obtained from information present in only one run of the dance. As stated previously, this type of averaging, if present, would have limited value because the between-bees component of the error could not be erased by averaging.

The contradiction of results between the step-experiments and the signal given by the dance (from the von Frisch & Jander study and this present study) may actually be due to a factor other than an "averaging" by receiving bees. As Haldane & Spurway (1954) suggest, a standard deviation for each step-experiment cannot be accurately computed since the scent posts

were not equidistant. On the other hand, von Frisch & Jander, in leaving out data on those bees which were killed at the feeding station, probably arrived at an over-estimate, rather than an under-estimate, from the data they had used.

Although an uneven spacing of scent posts reduces the accuracy of the estimate of standard deviation, it can have a much more serious effect in the particular experiments that were performed. Von Frisch & Jander do not indicate whether or not bees arriving at all scent posts were captured when they were counted, but von Frisch (1960) states that, except for those visiting the feeding station itself, they were neither captured nor marked. Thus despite von Frisch's opinion that bees were unlikely to visit more than one scent post, they were free to do so; and, in the time of the experiment, bees had ample time to visit all scent posts (in the 750 m. step-experiment, observations covered 90 minutes). If bees, after leaving one post without finding food, search more or less at random until they locate another post, an uneven spacing of posts can warp the frequency distribution of bee performance considerably.

Since enough of the necessary data is available, a critical comparison can be made between the expected results of the 750 m. step-experiment and those results actually obtained by von Frisch. Since the straight run times for any one distance (obtained either by the study of von Frisch & Jander or by this present study) fell into a normal curve distribution, one would expect recruited bees to perform in a normal curved distribution pattern; as stated before, this pattern should include the error of dancing bees and of recruited bees. For purposes of this comparison, however, recruited bees will be assumed to perform without error. Fig. 8a shows the hypothetical distribution at scent posts and at the food place (arranged as von Frisch had done in the 750 m. step-experiment) for 2,475 bees which had responded without error to the dance information. This distribution was calculated by using the standard deviation of the present study (for the data from the 700 m. distance) and a table of the areas of a normal curve. (A bar graph has been used here to compensate for the unequal spacing of scent posts. The bar graph will have a similar shape whether scent posts are equally or unequally spaced—a line graph will change shape according to the spacing of scent posts.) The actual results of von Frisch have been replotted in Fig. 7b for comparison. By comparing the two graphs (Figs.

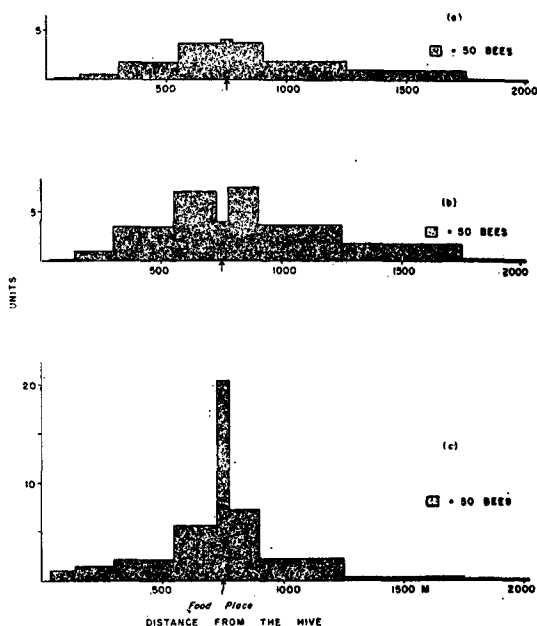


Fig. 8. Three hypothetical distributions of bee performance according to a normal curve distribution or modifications thereof:

7b and 8a), one can see that bees seem to be performing with more accuracy than would be expected, even when they are assumed to react to the given information without error.

Two simplified possibilities can now be considered: (1) Recruited bees revisit the station they initially visited; and (2) Recruited bees visit some station other than the one they initially visited.

Fig. 8b shows the expected change from the hypothetical distribution of Fig. 8a if each of the bees which had visited a scent post left and later reappeared at the same post. The dip in the centre of the graph results from killing those bees which had initially visited the feeding station. The apparent number of bees has increased to 4,756.

Fig. 8c shows the expected change from the hypothetical distribution of Fig. 8a if each of the bees which had visited a scent post then visited another scent post (i.e. if they searched at random and came to the next closest one proportionately but did not travel more than 500 m. from the first post they had visited). Even though bees coming to the feeding station were killed, no dip is present in this graph. Instead, the number of bees visiting the feeding station is disproportionately greater than that number

visiting the other stations. The unique shape of the graph is in part due to the peculiar arrangement of the unequally spaced stations. This unique shape is remarkably similar to those results obtained by von Frisch in his 750 m. step-experiment (Fig. 7b). Even if bee performance had double the error used here, an average of three scent posts visited per bee will give a distribution similar to that observed by von Frisch.

On the basis of the above model and discussion, a comparison between the data on what might be a signal for distance information and actual performance of bees in the field should not be made until step-experiments have been conducted which exclude the possibility of bees visiting more than one station.

The Possibility of Sound Communication by Honey Bees

The evidence presented in this paper shows that honey bees produce sound while dancing and may use this sound in communicating information about the distance of a food source from the hive. The evidence does not prove or disprove whether or not bees can receive sound; neither does it establish whether or not bees convert the time sound is produced during the straight run into a time of flight.

Frings & Frings (1958) reviewed and discussed the literature on the relationship between honey bees and sound. The findings by the researchers they cite generally indicate that there is a lack of response by bees to airborne sounds of normal intensity, but there is evidence for response to substrate sounds.

Simple experiments can be done which support the contention that bees perceive substrate sounds but not airborne sounds. If one shouts or claps his hands near a hive, bees usually do not respond to the noise. If, however, one stamps his feet or taps the hive with the hand or a hard object, the hive is immediately disturbed. More subtle disturbances are sometimes observed. For example, while the present study was being conducted, bees sometimes stopped their dancing when close-flying airplanes produced a vibration in the substrate. Also, von Frisch & Jander mounted their camera equipment on shock absorbent material after they found that noise produced by the motion picture camera stopped bees from dancing (Boch, 1959).

Results of simple experiments such as these are reinforced by the findings of Lindauer & Kerr (1960), in which they establish that stingless

bees not only perceive sounds but probably use these sounds in communicating information about food sources to each other.

If honey bees use sound in communication, the mechanics of production and reception have yet to be solved. Pumphrey's discussion on hearing in insects (1950) and Ribbands' discussion on hearing, vibration perception and sound production of bees (1953; chap. 6) include the possibilities and arguments about sound production and reception. Recent work by Slifer (1960) adds the possibility that the plate organs, being impermeable to chemicals, are not olfactory organs as von Frisch has stated (1950), but may function in sound reception.

Observations of dancing bees and their followers indicate an intimate contact between dancing bees and possible recruits. Von Frisch (1924) states that bees try to keep their antennae touching the dancing bee's abdomen and try to follow close behind her. He also states that a dancing bee exercises a wagging movement of the abdomen by which she beats the faces and antennae of the bees which are following. Although few bees were studied as they followed the dancing bee during this present study, observations of motion picture films verify the observations of von Frisch. In addition, one worker was seen to be postured at right angles to the straight run direction of the dancing bee while the wagging abdomen of the dancing bee beat the antennae and head of the waiting bee; this occurred at least three runs in succession. These observations lead to a consideration of the distinction between sound reception and touch reception.

Since the hive is virtually dark, a mechanical stimulation is more probably the conveyor of distance information than a visual stimulation. Pumphrey fully discusses the subtle distinction between sound reception and touch reception, concluding that the former is involved when the stimulus has a definite wave form and the latter when the stimulus is from an irregularly applied pressure. However, a reception of the wagging of the abdomen or of sound pulses may both be construed as reception of a definite wave form.

Only experimentation can decide whether the number of waggles, time of wagging, number of pulses, time of sound production, or a combination of these elements which occur during the straight run is the best explanation for the stimulus used by bees in conveying distance information—if one of them is used in communication.

An experiment which adds to our knowledge of communication between honey bees was performed by Steche (1957 *a* & *b*), in which he waggled an artificial bee in a glass-walled observation hive in an attempt to imitate the dancing of successful foragers. In this remarkable experiment he was able to stimulate bees to search for the nectar in the proper direction from the hive. A decision on whether or not information about distance of the food source was also communicated, however, awaits publication of his methods and data.

Summary

1. A pulsed sound of approximately 200 cps. which is produced during the straight run of the honey bee waggle dance is described. The presence of this sound provides a new possibility for explaining the method whereby information about the distance of the food source from the hive is communicated among bees. Besides the elements considered by von Frisch & Jander (1957), sound production time during the straight run and number of pulses present in the straight run are each shown to be also capable of carrying distance information. Since the ratio of the sound pulse rate to waggle rate is approximately 2.5 to 1, the sound is not an incidental result of wagging of the abdomen by the dancing bee.

2. The complete run time, straight run sound production time, and number of sound pulses were all graphically found to be more closely related to the distance of the food source from the hive than the circle run time. These three remaining components were not found to be significantly different from each other on the basis of raw data.

3. The results of a variation analysis of complete run time, straight run time, and circle run time indicate that variability of the complete run time can largely be attributed to variability of the circle run time.

4. The effect of wind is greater on the straight run time than on either complete run time or circle run time. Also, that variability in the complete run time which is due to an effect of wind can largely be attributed to the effect of wind on the straight run time. This information, together with that from 3 (above), shows that the average complete run time is mainly a sum of average circle run time and average straight run time and probably does not transmit distance information in its own right. Since the average complete run time of this study must be

equivalent to the average complete run time of the study of von Frisch & Jander, the complete run time of their study can also be eliminated as a possibility for transmitting distance information.

5. The straight run time and number of sound pulses present in the straight run were found to be inseparable on the basis of available data. Either of these two components was found to be a better possibility for transmitting distance information than any of the other components of the dance which were covered in this study. Neither of these two components can be directly compared to the straight run waggle time or number of waggles produced during the straight run (von Frisch & Jander, 1957). Such a comparison must await further experimentation.

6. The following four components (or a combination of any of these four) of the honey bee waggle dance now remain as best possibilities for conveying the information about distance of the food source from the hive:

- (a) time of wagging during the straight run.
- (b) number of waggles produced during the straight run.
- (c) time of sound production during the straight run
- (d) number of sound pulses produced during the straight run.

7. Analysis of wind effects reveals that bees signal the flight time out to the food source, not the flight time of the return trip.

8. The sound pulse rate did not vary appreciably with temperature. Although the sound pulse rate did vary with distance, the amount of change was slight and the significance was marginal.

9. The interpretation of the results of the step-experiments (Stufenversuchen) of von Frisch and co-workers is questionable, since a performance much poorer than that given by the standard deviation of the results, coupled with bees visiting more than one of the unevenly spaced stations, would give similar results.

10. The possible use of sound by honey bees in communicating information about the distance of a food source from the hive is discussed.

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