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THE DANCES OF HONEYBEES AT SMALL ZENITH DISTANCES OF THE SUN

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INTRODUCTION

A worker honeybee that has discovered a good food-source normally indicates the direction of this source to the other bees in the hive by performing a dance on the comb such that the angle between the direction of the dance and the vertical is equal to the angle between the azimuth (compass direction) of the food-source and the azimuth of the sun (von Frisch, 1946, 1948). If the direction of the food-source remains constant the direction of the dance must alter progressively during the day to compensate for the movement of the sun across the sky. If the path of the sun lies to the south the appropriate alteration of the dance direction is anticlockwise; if north, clockwise (see Fig. 1).

In the tropics, where the sun is north during part of the year and south during the remainder, the direction in which the dances turn† will depend on the season and latitude. At some time during the spring anticlockwise turning will give place to clockwise turning when the daily path of the sun has moved from south to north of the observer. Theoretically this alteration should take place within two successive days; on one day the sun will be very slightly south and on the next day very slightly north. In autumn the same will apply except that the change will be in the opposite direction.

On days near the north to south (or south to north) change the sun approaches very close to the zenith at noon each day. This makes it very difficult for the bees to determine accurately its azimuth, because at such times a very slight error in perception of the relative positions of the sun and zenith will lead to a very large error in estimation of sun azimuth. Moreover, the sun azimuth at these times is altering rapidly and at a varying rate (Fig. 1).

Lindauer (1957) concluded from observations in Ceylon that the bees' dances are disorientated when the sun passes within 2·5° of the zenith. We made some preliminary observations on a colony in Jamaica at the times that the sun was near the zenith during May 1960. Our observations began 2 days after the sun had passed north (noon zenith distance 0·5° N.) and we found that the dances in our colony, although deviating widely from the angle between sun and food-source, were not disorientated. They were well orientated right through the noon period and appeared to be turning in an anticlockwise direction, i.e. as though the sun were still south. It was not until several days later that clockwise turning was fully established. This suggested

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† 'Turning of the dances' is used in this paper to mean the progressive rotation of the angle indicated by a series of dances.

that bees might solve the problem of communication at small zenith distances of the sun by dancing to sun positions memorized from a few days previously. The problem appeared of great interest and we have therefore carried out further observations of the dances when the sun was close to the zenith, at three different localities. The following is an account of this work.

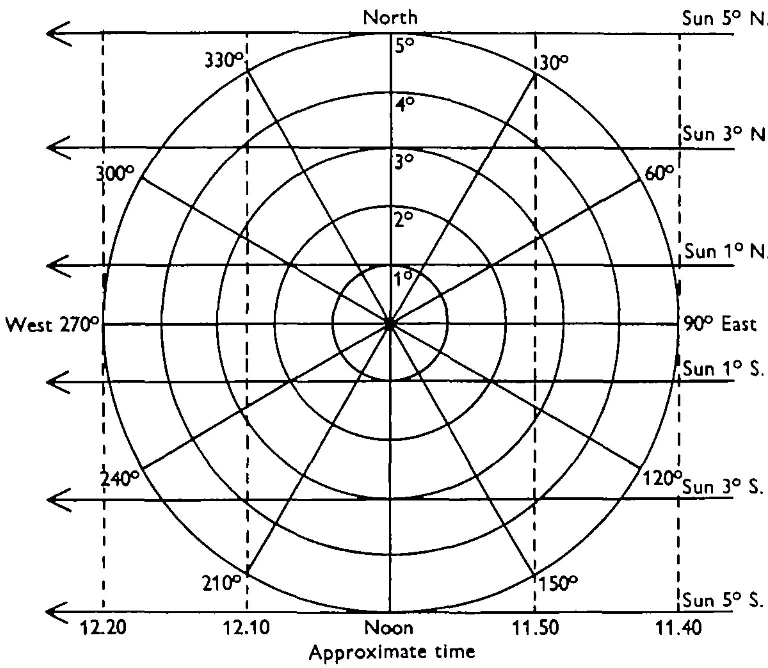

Fig. 1. Sun paths close to the zenith. Circles indicate zenith distances; radii indicate azimuths. The closer the sun passes to the zenith the more rapidly the azimuth changes around noon. (The times given are accurate for the Equator but vary by a minute or two at other places in the tropics.)

METHOD

On days when the sun passes close to the zenith at noon most of its change of azimuth occurs between 11 a.m. and 1 p.m.* and only small changes occur during the rest of the day (Fig. 1). This means that the direction of the bees' dances has to alter rapidly during the noon period and it becomes apparent in a fairly short time whether the dances are turning clockwise or anticlockwise. Accordingly, most of our observations were made around this time of day.

Observations were made in three localities: Tukeit, British Guiana (5° 11′ N.); St Augustine, Trinidad (10° 38′ N.); Mona, Jamaica (18° 00′ N.).

In Trinidad and Jamaica the observations were made on local bees. The bees used at Tukeit were brought from Georgetown (6° 50′ N.) a few days before observations were started.

The bees were housed in small 2-comb observation hives; the hives were kept indoors and each hive entrance was connected by a small tunnel with a hole in the wall

* All times given in this paper are true solar times such that the sun always crosses the meridian of the observer at noon.

of the room. A metal deflector in the entrance of each hive directed all incoming bees on to one face of the comb and only this side of the hive was opened to the light. Illumination of the dances was by diffuse white light from an electric bulb placed behind the hive and reflected onto the bees from a facing wall. The light was kept as dim as possible and at an even intensity of illumination over the area of room visible to the bees. As a final check that the illumination was not affecting the gravity-orientation of the bees' dances several control experiments were carried out in which the angle of the dances was determined while the sun was fairly low in the sky. In a typical experiment of this kind 69 dances were recorded; the mean error from the expected* direction was only 5°.

The feeding dish to which the bees were trained was usually placed about 400 m. from the hive and supplied with strong sugar syrup so that the bees performed vigorous and well-orientated dances. The direction of the dance was recorded by laying a thread on the glass side of the hive along the line of the 'waggle run' of the dancing bee and then measuring with a protractor the angle between this thread and another orientated in the vertical by means of a plumb line. At no time did the observer have more than the vaguest idea of what the expected dance should be. Sun azimuths and hence the expected angles for the dances were only calculated after all the observations had been made in the particular locality.

Sun azimuths were calculated round the astronomic zenith, i.e. the zenith defined by the direction of gravity. The possibility that the bees might estimate sun azimuths round a different zenith will be considered in the discussion.

RESULTS

In general, when the sun was within three or four degrees of the zenith the bees performed fewer dances than at other times and some bees danced less vigorously. Occasionally the bees ceased dancing altogether or performed a series of movements which might have represented 'disorientated dances'. On these occasions they resembled the bees observed by Lindauer (1957) in Ceylon. But this was unusual. As a rule dancing continued throughout the noon period. A few bees while performing a dance would vary the angle more than normally, sometimes wavering through as much as 90°; in such cases the mean of the angles indicated was recorded. Other bees would give excellently orientated dances however close the sun was to the zenith. Completely disorientated dances, in the sense of clearly executed waggle runs in all directions, were very rare.

The results for the different localities are as follows:

Tukeit (5° 11′ N.)

Sun overhead: 2, 3 April.

Position of food-source: S.E.

Site: steep-sided valley running S.W.–N.E. Slope of ground altering rapidly and unevenly. Mainly forest covered.

* 'Expected direction of dances' refers in this paper to dances indicating the angle between the azimuths of the food source and of the immediate sun position.

Nearly all the foraging bees in this colony were collecting pollen (of which the hive was very short) and all attempts to train them in the short time available to a feeding dish of syrup failed. Fortunately the great majority of the foragers were collecting a yellow pollen from sources in approximately the same direction S.E. of the hive, and the collecting continued over the midday period. Thus by recording the dances of these foragers at this time it was possible to see whether they were changing in a clockwise or anticlockwise direction.

The last day on which the sun path lay to the south of the locality was 2 April. The first records of the dances were taken on 3 April on which day the sun path lay slightly to the north. Further records were taken on 4 and 5 April and the combined

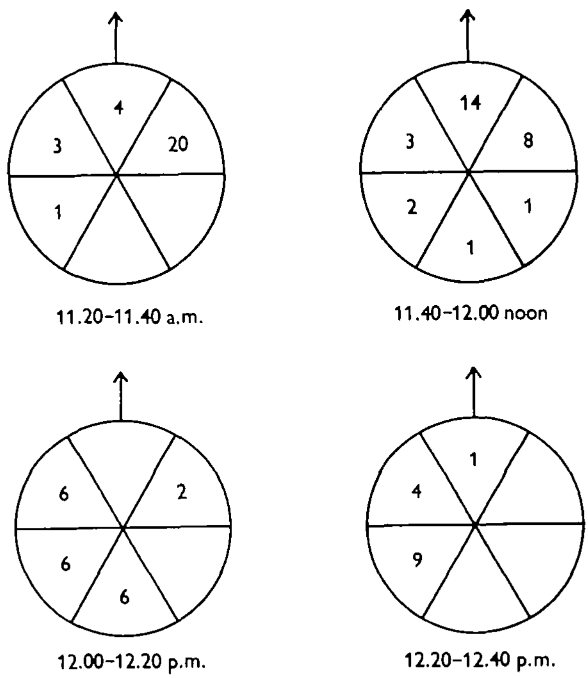

Fig. 2. Dance angles given by bees at Tukeit. The arrows indicate the direction of the vertical (upwards) on the comb. Figures show the number of dances within each 60° sector.

results of all 3 days are summarized in Fig. 2. Shown in the figure are the numbers of dances within each 60° arc during each 20 min. period from 11.20 a.m. to 12.40 p.m. Between 11.20 and 11.40 most of the dances were orientated between 30° and 90° to the right of the vertical. By 12.20 to 12.40 the most favoured direction had become 90°–120° to the left. A change of direction of the order of 180° had occurred in about 1 hr. Examination of Fig. 1 shows that this is well in accordance with the change of sun azimuth (sun paths < 1·0° N). But the most striking feature of the change shown in Fig. 2 is that the majority of, and possibly all, the bees have progressively turned their dances round in an anticlockwise direction. This would be expected if the path of the sun lay to the south; but during all 3 days on which these observations were made the sun was to the north.

The decline in total numbers of dances recorded in Fig. 2 is a reflexion of a steady decline in pollen collecting which occurred around noon each day. Numerous loads of pollen were seen arriving during the morning but very few after 1 p.m. Between 12.00 and 12.40 all the dances performed were recorded. Before 12.00 more dances were performed than could be recorded, and it was necessary to allow for the effects of selection on the part of the observer. The rule followed was that if two or three bees, all with loads of yellow pollen, were seen dancing simultaneously, measurements would be made on the bee that deviated most from the dance direction given by the majority of the bees around that time. The first two circles in Fig. 2 therefore exaggerate if anything the scattering of the dance directions. The fact that in spite of this the figures clearly show an anticlockwise trend in the turning of the dances indicates strongly that the bees are dancing as though to a southern sun.

Trinidad (10° 38′ N.)

Sun overhead: 17, 18 April.

Colony no. 1

Position of food-source: E.N.E. (azimuth 65°), 420 m. from hive.

Site: level turf sloping slightly downwards to S.W. A few buildings in the line of flight.

A small group of bees were trained to the feeding dish, then marked and numbered. Only the dances performed by these marked bees were recorded.

Records of the dances were made on 7 days between 15 and 22 April. Fig. 3 shows the results on 3 days when the sun was south and on 3 days after it had passed north. A surprising feature of the dances was that on all days they turned clockwise—appropriate to a northern sun. For the first 3 days, therefore, they were apparently predicting future sun movements; there could not here be any possibility of orientating the dances by memorized sun movements because none of these bees had ever experienced a sun in the north.

Another consistent feature of the dances in this colony was that when the dance angles were plotted against time they produced curves symmetrical about noon but of smaller maximum slope than the curves of expected dance angles (Fig. 3). This was true even when the observed and expected dances were turning in opposite directions.

Two of the best series of dances given by individual bees are shown in Fig. 6.

Comment on these results will be left to the Discussion.

Colony no. 2

Position of food-source: S.E., 220 m. from hive.

Site: same as colony no. 1.

In view of the surprising results obtained from colony 1 during the first few days in Trinidad it became desirable to have a parallel set of observations made on another colony. This second colony had to be set up hurriedly in an observation hive in the open and the dancers had full view of the sky. However, as the sun was never more than 10° from the zenith during the period of observations the light would only alter the orientation of the dances by amounts up to 5° (von Frisch, 1948) and would not affect observations on whether the dances were turning clockwise or anticlockwise through an angle of about 170°.

The dances were classified as shown in Fig. 4. All dances were ignored that occurred within 20° of either the expected direction for 11.30 a.m. or the expected direction for 12.30 p.m. Dances that indicated angles outside these limits were regarded as evidence for clockwise or anticlockwise turning. The results are shown in Table 1. On 20 April of the six marked bees dancing over the midday period four were clearly

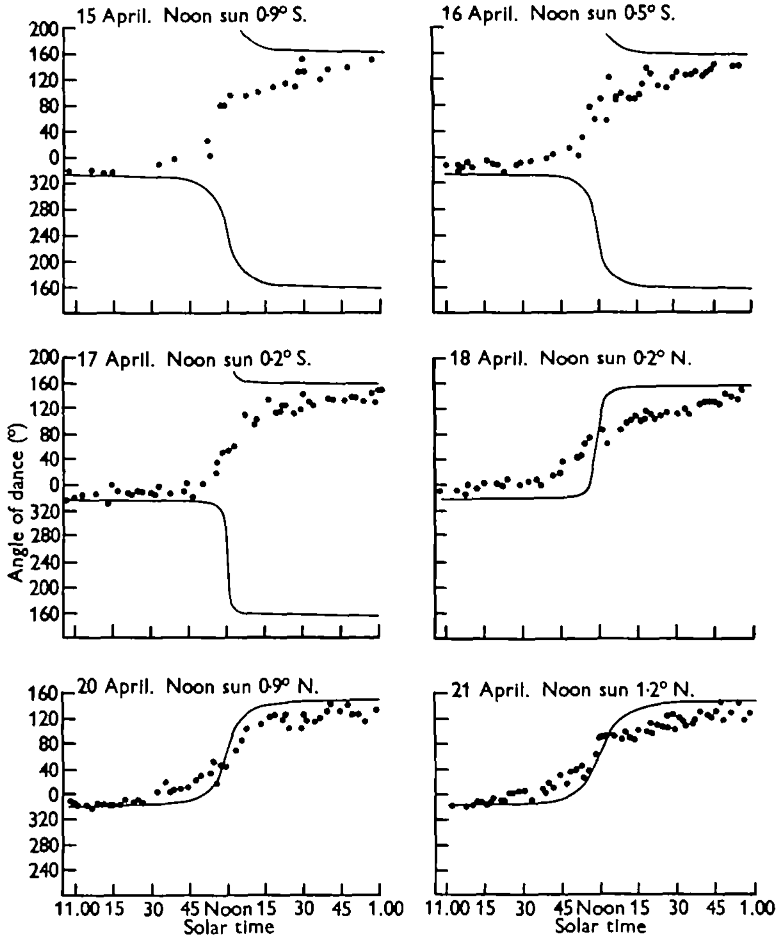

Fig. 3. Colony 1, Trinidad, 15–21 April. The sun passed 0·9° south of the zenith on the first day, and 1·2° north of the zenith on the last day. Separate points indicate the dance angles observed. Continuous lines indicate the angles of 'expected' dances, i.e. the angles between the azimuths of the sun and the azimuth of the feeding dish. 0° represents vertically upwards on the comb and all dance angles are measured clockwise from this.

turning anticlockwise and none was turning clockwise. Two of these bees were still turning anticlockwise on 22 April, the fifth day after the sun had passed north. This is in marked contrast to colony 1 where no bee was seen to turn anticlockwise on any day from 15 to 21 April. Although both colonies were on the same site colony 1 was apparently dancing to a northern sun whilst the sun was still south, and colony 2 was apparently dancing to a southern sun after the sun had passed north.

Jamaica (18° 00′ N.)

Sun overhead: 11, 12 May.

Position of food-source: N.E. (azimuth 45°), 400 m. from hive.

Site: residential area: Line of flight over houses, gardens, roads. Fairly level ground sloping downwards to S.W.

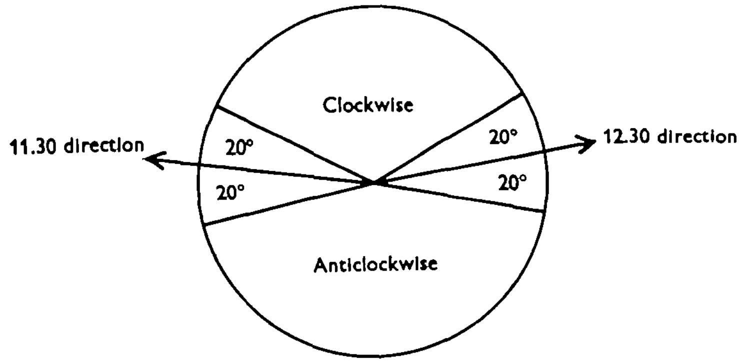

Fig. 4. Method of classification of dances performed between 11.30 a.m. and 12.30 p.m. into 'clockwise' and 'anticlockwise'.

Table 1. *Colony 2, Trinidad. Clockwise and anticlockwise dancing bees*

(Classified as shown in Fig. 4.)

Date	Noon sun	Marked bees missing or not dancing. Bee no.	Extra bees marked. Bee no.	Direction of turning: Anti-clockwise. Bee no.	Uncertain. Bee no.	Clockwise. Bee no.
20 April	0·9° N.	1	—	2	6	—
		3	—	4	8	—
		5	—	7	—	—
		9	—	10	—	—
21 April	1·2° N.	3, 5	11	2	1	6
		8	12	4	—	11
		9	13	7	—	14
		10	14	12	—	15
		13	15	—	—	—
22 April	1·6° N.	3, 5	16	2	4	1
		8, 9	—	7	—	6
		10, 12	—	—	—	11
		13	—	—	—	15
		14	—	—	—	16

Two colonies were observed in Jamaica. They were housed in the same darkroom and a small group of marked bees from each were trained to the same feeding dish. The marked bees from the two colonies were presumably therefore following the same line of flight. The sun moved from south to north between 11 and 12 May, and observations of the dances were made on most days between 8 and 19 May.

The dances around midday in Jamaica were less uniform than those of colony 1, Trinidad. On some days very few dances were performed between 11.45 a.m. and 12.15 p.m. On other days a large number of well-orientated dances were performed, but sometimes a few bees were turning clockwise whilst others were turning anticlockwise. The dances performed between 11.30 a.m. and 12.30 p.m. were classified according to Fig. 4 and are listed in Table 2. The table shows that in general anticlockwise turning is dominant until several days after the sun has passed north, but is being replaced by clockwise turning by about 18 May. There are a few records of

Table 2. *Dances performed by individual bees on successive days in two colonies in Jamaica*

(Classified into clockwise (C) and anticlockwise (A) as shown in Fig. 4. The figures indicate the number of dances between 11.30 a.m. and 12.30 p.m. that could be clearly classified.)

Colony 5

Date	Noon sun	Bee no. 1	2	3	4	5	7	8	9	10	11	12	13	14
8 May	0·9° S.	3A1C	3A1C	2A1C	4A	4A	—	5A	3A	1A	1A	—	—	—
10	0·4° S.	2A	2A	—	—	—	5A	4A	—	—	—	3A	5A	1A
11	0·1° S.	1A	—	—	—	—	—	—	—	—	1A	—	—	3A
12	0·1° N.	—	—	—	—	—	3A	2A	—	—	1A	—	2A	—
14	0·6° N.	—	—	—	—	—	1A	1C	—	—	1A	—	1C	—
15	0·9° N.	—	—	—	—	—	3A	4A	—	—	4A	—	8A	—

Colony 6

Date	Noon sun	Bee no. 1	2	3	4	5	10	11	12	13	14	17	18	20
9 May	0·7° S.	1C	—	1A	1A	3A	4A	1A	—	—	—	—	—	—
10	0·4° S.	—	—	—	2A	4A	—	—	—	—	—	—	—	—
11	0·1° S.	—	1A	—	1A	5A	—	—	—	—	—	—	—	—
12	0·1° N.	1A	—	—	1A	3A	—	—	—	—	—	—	—	—
14	0·6° N.	—	—	—	1C	1C	—	1A	2C	—	—	—	—	—
15	0·9° N.	—	—	—	4A	2A	—	5A	2A	3A	3A	—	—	—
16	1·1° N.	—	—	—	2A4C	—	—	2A	3A2C	2A	1A	3A	2A1C	2A
18	1·5° N.	—	—	—	3C	—	—	—	3C	2A1C	1A1C	—	—	3C

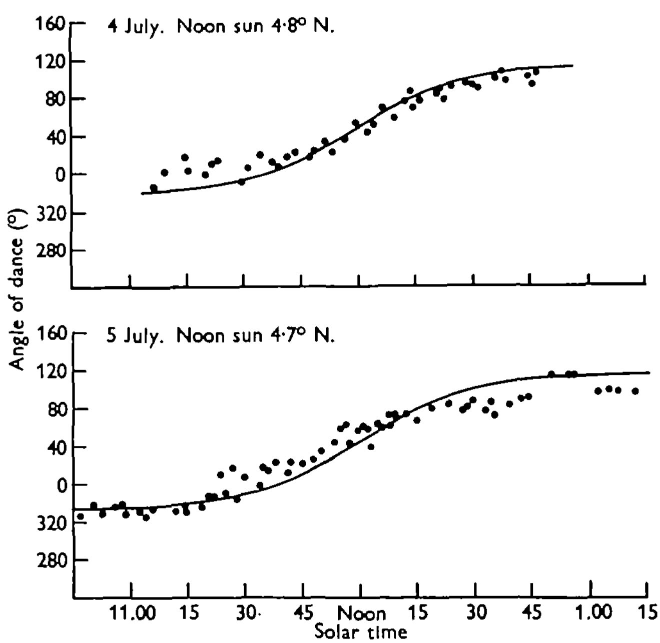

Fig. 5. Colony 5, Jamaica, 4 and 5 July. Separate points indicate observed dance angles. Continuous lines indicate 'expected' dance angles. Dances measured as in Fig. 3.

individual bees (e.g. colony 6, bee no. 4) having changed from anticlockwise to clockwise turning.

Further observations were made on 4 and 5 July, at which time the zenith distance of the noon sun was $4\frac{3}{8}°$ N. The colony of bees was one of those used previously (no. 5) and the feeding dish was set up at the same place. The results are shown in Fig. 5. The turning of the dances is now entirely clockwise but it is still noticeable that the maximum slope of the curve of observed dances is less than the maximum slope of the curve of expected dances.

Table 3. *Dances performed by individual bees on three successive days in Jamaica*

(Classified into clockwise (C) and anticlockwise (A) as shown in Fig. 4. The figures indicate the number of dances between 11.30 a.m. and 12.30 p.m. that could be clearly classified.)

Date	Noon zenith distance of sun	Bee no. 1	2	5	6	7	10	17	19
23 July	2·1° N.	3A1C	2A1C	1A2C	1A1C	—	—	—	—
24	1·9° N.	2A	1C	1A1C	—	1C	6A	—	—
25	1·7° N.	2A	2C	1C	—	—	1A	1C	1C

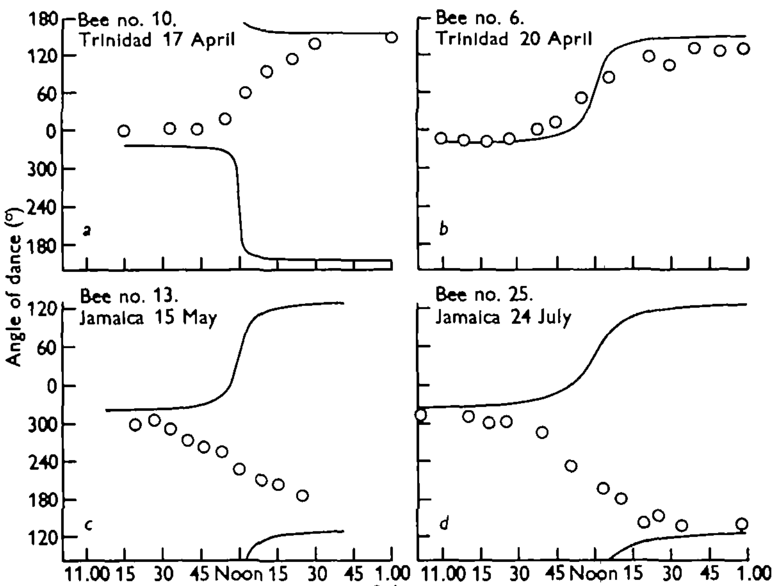

Fig. 6. Four records of dances performed by individual bees. Circles show observed dance angles. Continuous lines show 'expected' dance angles. Dances measured as in Fig. 3. *a*, A bee dancing 'to a northern sun' before the sun has moved north; *b*, the dances turn in the expected direction but the curve of the observed dances is less steep than the curve of the 'expected' dances; *c*, a bee dancing 'to a southern sun' after the sun has moved north; *d*, a bee dancing 'to a southern sun' before the sun has moved south.

A final set of observations was made 23–25 July by which time the sun was again $1\frac{1}{2}°$–2° north but now moving southwards. The dances between 11.30 and 12.30 were classified as before into clockwise and anticlockwise, and the results are shown in Table 3. Bee no. 1 and bee no. 10 had evidently changed to anticlockwise dancing, as though predicting sun movements several days ahead (cf. colony 1, Trinidad). The others appeared uncertain, but tended towards clockwise.

Two of the best series of dances performed by individual bees in Jamaica are shown in Fig. 6.

Summary of results

A summary of the results obtained at Tukeit, Trinidad and Jamaica is given in Table 4.

Table 4. *Summary of directions of turning of dances observed in different colonies at different localities in* 1961

	Sun moving North					Sun moving south,
Noon sun	Tukeit	Trinidad, colony 1	Trinidad, colony 2	Jamaica, colony 5	Jamaica, colony 6	Jamaica, colony 5
4·8° N.	—	—	—	—	—	Clock
4·7° N.	—	—	—	—	—	Clock
2·0° N.	—	—	—	—	—	Mixed
	—	—	—	—	—	Mixed
1·5° N.	—	Clock	Mixed	—	Mixed	Mixed
	—	Clock	Mixed	—	—	—
	—	—	—	—	Mixed	—
1·0° N.	Anticlock	Clock	Anticlock	—	—	—
	—	—	—	Anticlock	Anticlock	—
0·5° N.	Anticlock	—	—	Mixed	Mixed	—
	—	Clock	—	—	—	—
	Anticlock	—	—	Anticlock	Anticlock	—
0·0						
	—	Clock	—	Anticlock	Anticlock	—
0·5° S.	—	Clock	—	Anticlock	Anticlock	—
	—	—	—	—	Anticlock	—
1·0° S.	—	Clock	—	Anticlock	—	—

DISCUSSION

Three main conclusions emerge from the work that has been described.

(1) Some of the foraging bees continue to perform orientated dances however close the sun moves to the zenith.

(2) The dance angles plotted against time give smooth curves symmetrical about noon but of smaller maximum slope than the curves of expected dances.

(3) The direction of turning of the dances is often opposite to the expected direction.

In view of the extreme difficulty of measuring accurately the azimuth of the sun when it is near the zenith it is remarkable that the bees are able to continue performing dances orientated within fairly narrow limits. Most behavioural studies of visual acuity of bees (e.g. Hecht & Wolf, 1929) have indicated a resolving power of about 1°, a value that would make it impossible for the bees to have more than the vaguest impression of sun azimuth when the sun was within a few degrees of the zenith. Recently the work of Burtt & Catton (1954, 1959, 1962) has suggested that the resolving power of the insect compound eye may be as little as 0·1°. If bees are able to locate the sun position (and the position of the zenith) as accurately as this, then they should certainly be able to perceive the azimuth of the sun with reasonable precision until the sun was within a fraction of a degree of the zenith. But in that case why should the curves of observed dance angles (Figs. 3, 6) differ so markedly from the curves of expected dance angles?

One possibility is that the zenith used by the bees is different from the astronomic zenith (which has been used here in the calculation of expected dances). The curves given by the observed dances often correspond closely to the curves expected if the sun azimuths had been calculated round a zenith situated a little north or south of the astronomic zenith. For example, the dances given by colony 1, Trinidad (Fig. 3) would agree well with sun azimuths calculated round a zenith 3° S. of the astronomic zenith.

The astronomic zenith is defined by the direction of gravity. A conceivable alternative zenith could be obtained by projecting the perpendicular to the ground surface. In Trinidad the ground sloped evenly to the S.W. at an angle of about 0·7° from the horizontal. Therefore a zenith based on the perpendicular to the ground would be 0·7° S.W. of the astronomic zenith. If the bees used such a zenith it might well lead to them dancing to a northern sun before the sun had passed north as occurred in colony 1; but it would not explain why colony 2 behaved differently. And in Jamaica this explanation would predict the opposite of what was observed; here the slope of the ground was also to the S.W. but the bees did not change to dances appropriate for a northern sun until some days after the sun had passed north of the astronomic zenith.

Evidently a zenith based on the perpendicular to the ground surface cannot be an explanation of the observed dances. But could some other method be used by the bees for determining a non-astronomic zenith? Any such method would have to allow for different colonies in the same locality using different zeniths (to account for the results in Trinidad); and such zeniths would have to be due north or due south of the astronomic zenith but not appreciably east or west, because the curves of observed dance angles are symmetrical about noon. It seems extremely unlikely that bees should have evolved such peculiar methods of assessing zeniths, particularly as such zeniths would seem to have no advantages over the astronomic zenith which presumably they are able to determine by means of their gravity receptors (Lindauer & Nedel, 1959). A final reason for rejecting the displaced-zenith hypothesis is the fact that in Fig. 5 the maximum slope of the curves of observed dances is less than the maximum slope of the curves of expected dances. If the observed dances are related to a non-astronomic zenith the slope of the curves indicates that it would have to be farther to the south than the astronomic zenith. But 8 weeks earlier dancers in the same colony working at the same feeding dish had behaved as though their zenith were north of the astronomic zenith (Table 2, colony 5). If these bees were working to a non-astronomic zenith then they must have changed its position during the course of 8 weeks. The supposition that bees assess sun azimuths round a non-astronomic zenith clearly leads to great difficulties.

If the bees are not estimating sun azimuths round the astronomic zenith, or any other zenith, what is it that causes them to alter the direction of their dances so systematically? Recent work which has suggested that bees are able to extrapolate the curve of sun movement is of great interest. Lindauer (1957, 1959) has shown that bees that have only been allowed to observe the path of the sun during afternoons are nevertheless able to use it for navigation immediately they are released in a morning. Furthermore, following up an observation by Wittekindt (1955) that bees can be induced to dance after sunset, Lindauer (1957) has shown that the dances performed at any time during the night indicate approximately the angle between the daytime food source and the azimuth of the sun at the particular time of night. In both these cases it is conceivable that the bees perceive some non-visual information from the environment as to the sun's position, but a much more likely explanation is that given by Lindauer, that they extrapolate the complete 24 hr. circle of azimuth change from the part that they are able to see.

However, in attempting to use an explanation of this kind for dance orientation when the sun is close to the zenith the difficulty arises that a very different azimuth curve is involved. Fig. 7 compares the types of azimuth curve of the summer sun in Central Europe, where Lindauer's extrapolation experiments were carried out, with the types of azimuth curve obtained in the tropics on days when the sun passes close

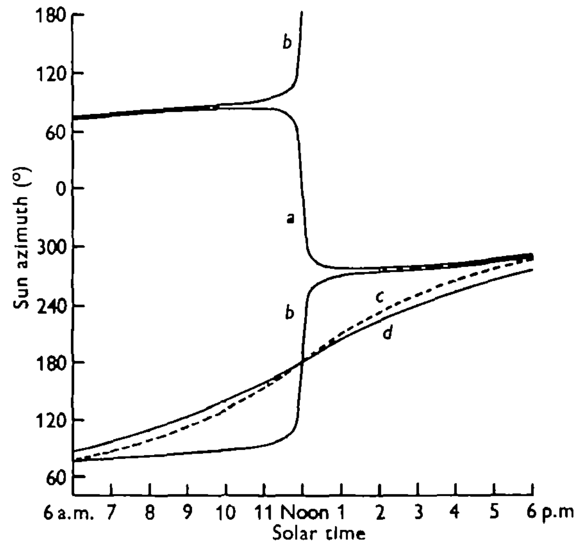

Fig. 7. *a*, *b*, Typical azimuth curves when the sun passes close to the zenith. In Jamaica the sun changes from *a* to *b* in about 8 days. The azimuth changes very rapidly around noon but only very slowly for most of the morning and afternoon. *c*, *d*, Typical summer sun azimuth curves in temperate latitudes. The curves shown represent the limits of azimuth change between April and August at latitude 50° N.

to the zenith. Where the sun path is at a large angle south or north of the observer the azimuth curve approximates to a straight line with a rate of change of 15°/hr. Bees that had learnt part of such a sun path might therefore obtain an approximation to the remainder by extrapolating either forwards or backwards at the rate of 15°/hr. from the part they knew.

Where the sun path passes close to the zenith, however, the rate of change of azimuth varies widely at different times of day, and only for very short periods does it approximate to 15°/hr. (Fig. 7). For most of the morning, and for most of the afternoon, the sun only undergoes slight changes of azimuth and neither of these parts of the sun azimuth curve can be derived from the other by extrapolation, nor will either on extrapolation produce the type of azimuth curve that occurs around noon. If the bees' dances around noon (11.30–12.30) were based on a forward extrapolation of the morning sun azimuth curve, or a backward extrapolation of the afternoon azimuth curve (learnt on previous days) the average rate of turning of their dances during the noon hour would be less than a twentieth of the rate that actually occurs.

If the bees extrapolated not merely the azimuth curve but the path of the sun across the sky, i.e. took into account altitude changes as well as azimuth, then it would be theoretically possible for them to predict the sun path around noon from observations of its path earlier in the day. But this leads to the same type of difficulty as direct perception of the sun's position. Slight errors in extrapolating the sun path, or in assessing the position of the zenith, or in measurement of time, will all lead to large errors in the estimation of the sun azimuth. The result expected would be a wide scattering of dance angles around a curve whose slope is determined by the rate of change of sun azimuth, whereas the dances actually performed show a very limited scattering around a curve which is *not* based on the sun azimuth curve. Explanations based on extrapolation of the sun path or sun azimuth curve appear therefore unlikely to be correct.

The bees' flight must be affected by the prevailing wind, and it would not be surprising if the dances on the comb indicated the flight orientation necessary to compensate for any lateral displacement by the wind. This could lead to differences between the observed dances and the expected dances. Von Frisch & Lindauer (1955) have examined this possibility and have concluded that the dance angle is unaffected by the prevailing wind; the bees continue to indicate the true direction of the food source (and not the flight orientation) even when a strong side wind is blowing. Using data kindly supplied to us by the West Indies Meteorological Service in Jamaica and Trinidad we have examined our results for possible effects of wind, but we have been unable to find any correlation between either speed or direction of the wind and the deviations from the expected dances shown by the bees. The wind was in general very light during our experiments and was consistently east in Trinidad and south east in Jamaica.

Although the wind has no effect, small deviations in the dance angles arising from other causes have recently been described by von Frisch & Lindauer (1961). The magnitude of the deviations varies with the direction of the dance on the comb and appears to be a 'translation error' which arises in the change from light orientation to gravity orientation; it does not occur on a horizontal comb where the bees are orientating their dances by light. These deviations, however, are far too small (maximum 7°) to account for our results, and the dance directions on the comb where the 'translation errors' are zero are often the directions where we have obtained particularly large deviations.

None of the known mechanisms, therefore, accounts adequately for the dances performed by bees when the sun is close to the zenith, and it becomes necessary to look for an additional mechanism. A curious feature of the observed dances (Figs. 3, 5 and 6) is that as the sun approaches the zenith their acceleration in rate of turning precedes the acceleration in turning of the expected dances (based on changing sun azimuth). But after noon the observed dances lag behind the expected dances. It appears as though the turning of the observed dances were being influenced before noon by the bees' knowledge of the afternoon sun path (memorized from previous days), and after noon by the bees' knowledge of the morning sun path. This leads to the following hypothesis:

Dual-control hypothesis of dance orientation

The rate of turning of the dances is controlled by two mechanisms:

(1) A mechanism, as first described by von Frisch (1946, 1948), which uses all available information about the immediate sun azimuth. The accuracy with which this can be perceived will vary with the distance of the sun from the zenith, the amount of cloud over the sun, etc., and hence the deviation of observed dances from expected dances will vary from time to time. But it is unlikely that the bees will perform dances corresponding to sun azimuths outside the limits set by direct perception.

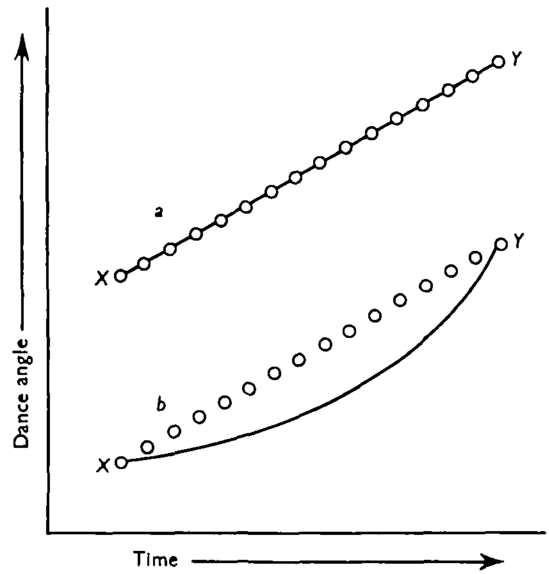

Fig. 8. Dual-control hypothesis of dance orientation. Continuous lines show dance angles set by observation of immediate sun azimuth; circles show dance angles set by the internal control mechanism. The bees have memorized from previous days the dance angles (or sun positions) at times X and Y. (*a*) If the sun azimuth changes at a uniform rate between X and Y the two control mechanisms reinforce each other. (*b*) If the sun azimuth does not change at a uniform rate between X and Y the two mechanisms will set different angles for the dances.

(2) A mechanism which takes into account the dance directions (or sun azimuths) memorized for particular times of day, and which between successive memorized positions attempts to turn the dances through an angle proportional to time. It will be convenient to refer to this mechanism as the 'internal control mechanism'.

When the sun azimuth is changing at a uniform rate the two mechanisms will reinforce each other (Fig. 8*a*), but when the rate of change is not uniform the two mechanisms will set different angles for the dances (Fig. 8*b*), and if temporarily the immediate sun azimuth cannot be perceived by the bees the observed dances (controlled now entirely by the internal mechanism) will differ from the expected dances (based on immediate sun azimuth). In temperate latitudes the sun azimuth curve shows only small deviations from a straight line (Fig. 7) and hence differences between observed and expected dances would be difficult to detect. Nevertheless, Lindauer (1957) has concluded from observations in Central Europe that the dances performed by bees at night turn at a uniform rate and not at the slightly varying rate corresponding with rate of change of sun azimuth.

In the tropics, where the rate of change of sun azimuth is much more variable, the internal control mechanism is revealed clearly. Fig. 9 shows the suggested interaction between the two control mechanisms at times when the sun passes close to the zenith. The stippled area represents the accuracy with which the bees could perceive the sun azimuth at different small zenith distances. This varies considerably with small changes in the acuity with which they can perceive the positions of both the sun and the zenith. In one of the diagrams in Fig. 9 the assumption is made that the relative positions of sun and zenith can be determined with an accuracy of 0·5°; in the other, that they can only be determined with an accuracy of 2°. (The limits of accuracy of sun-azimuth perception have been obtained from

$$\sin a = b/\text{zenith distance},$$

where a = azimuth limits and b = acuity of sun-zenith perception.) The continuous lines within the stippled areas are the curves of dance angles predicted by the dual-control hypothesis. These lines follow the shortest routes possible between the dance angles at successive times of day without going outside the stippled area.

It will be seen that the predicted curves are of the same type as those of the observed dances in Figs. 3, 5 and 6. They are symmetrical about noon and of smaller maximum slope than the curves of expected dances. Moreover, Fig. 9 shows that when the sun passes closer to the zenith than the minimum angle between sun and zenith that the bees can detect, the dual-control hypothesis predicts that the dances may turn either clockwise or anticlockwise, and therefore accounts for this very striking feature of the observed dances.

What is the acuity with which bees can perceive the relative positions of sun and zenith? Visual acuity is certainly not less accurate than 1° (Hecht & Wolf, 1929), but little information is available about gravity acuity (on which zenith perception depends) although gravity perceptors in bees have been described (Lindauer & Nedel, 1959). A value for this can be derived from the deviations of observed from expected dances when the sun is close to the zenith. The dances observed in colony 1, Trinidad (Fig. 3) while the sun was within 12° of the zenith have been compared with the curves of dance angles predicted by the dual-control hypothesis for different sun-zenith acuities between 0° and 5°. The results are shown in Fig. 10 and Table 5, from which it appears that the average accuracy with which the bees could determine the relative positions of sun and zenith over the whole period of the experiments was 2°–3°. (Statistical analysis of all the observed dances shows they fit the 3° acuity curve significantly better, at the 1 % probability level, than either the 1° or 5° acuity curves. At 3 % probability level they fit the 3° acuity curve significantly better than the 4° acuity curves.) This suggests that the acuity with which bees can locate a visual stimulus relative to the direction of gravity (i.e. the sum of their visual acuity and gravity acuity) cannot be less than 2°–3° and may well be greater under some circumstances, since in these experiments the bees would only be able to demonstrate their most accurate perception under optimum weather conditions.

The internal control mechanism which has been suggested agrees well with much that is already known about internal mechanisms in honeybees. That bees have a time

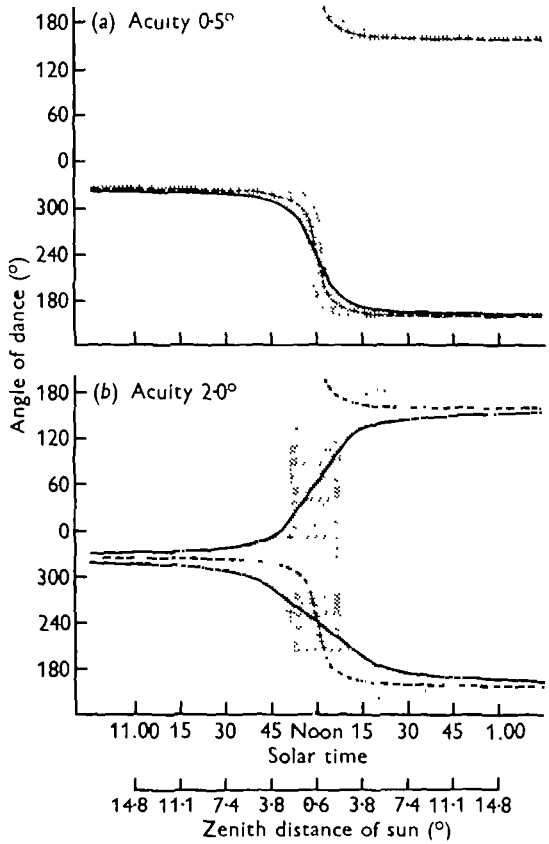

Fig. 9. Suggested explanation of dance orientation when the sun passes close to the zenith. Sun path is 0·6° S. of zenith. Broken lines indicate angles between azimuths of food-source and sun. Stippled area shows widening limits of accuracy of perception of sun azimuth as sun approaches the zenith. Continuous lines show the predicted dance angles: (*a*) if the bees can perceive the sun position relative to the zenith with an accuracy of 0·5°; (*b*) if the bees can only perceive the position of the sun relative to the zenith with an accuracy of 2·0°. In the latter case the hypothesis predicts that the dances may turn either clockwise or anticlockwise.

Table 5. *Calculation of mean deviations of dance angles from values predicted by the 'dual control' hypothesis for different acuities of sun-zenith perception.*

(The dances used are those observed in colony 1, Trinidad (Fig. 3).)

Acuity of sun-zenith perception ...		0°	1°	2°	3°	4°	5°
Sum of deviations of dance angles (a.m.)	15 April	515°	237°	101°	103°	141°	182°
	16	635	236	100	152	252	330
	17	453	130	153	288	404	493
	18	634	384	191	105	131	186
	20	302	132	159	282	387	475
	21	446	262	205	366	462	570
Sum of deviations of dance angles (p.m.)	15 April	603	342	210	122	107	159
	16	1040	626	415	264	220	217
	17	797	403	255	169	190	269
	18	896	603	359	197	154	173
	20	491	261	185	199	230	298
	21	765	520	310	255	230	285
Total deviations for 6 days		7577	4136	2643	2502	2908	3637
Total number of dances		217	217	217	217	217	217
∴ Mean deviation		34·9°	19·1°	12·2°	11·5°	13·4°	16·8°

sense independent of the environment is well established (Renner, 1955, 1957, 1959). That bees will occasionally dance for more than an hour without leaving the hive, and turn the dance meanwhile to compensate for sun movement, has also been observed (Lindauer, 1961, p. 95). And that bees can allow for sun movement sufficiently to navigate at one time of day by a sun that previously they have only seen at other times is indicated by Lindauer's (1957, 1959) work. But the dances performed when the sun is close to the zenith suggest that bees can do more than this. Apparently they can turn their dances systematically in a direction which could not have been learnt by observing sun movements, and which may not correspond with the changing sun azimuth occurring at the time, but which nevertheless takes into account dance directions (or sun azimuths) memorized for other times of day, and between successive memorized positions turns the dances through an angle proportional to time. In fact they appear to have an innate mechanism that can divide angles by time.

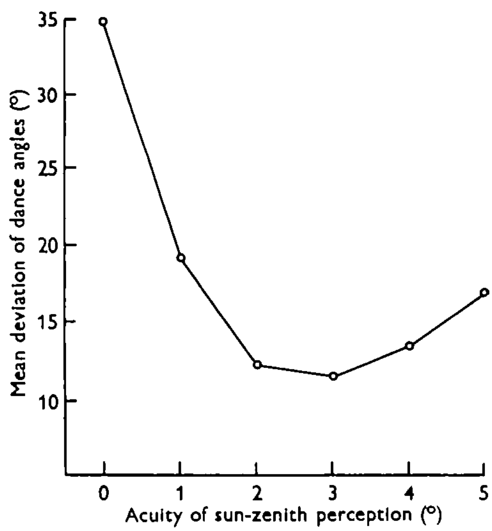

Fig. 10. Mean deviations of observed dance angles from the values predicted by the dual-control hypothesis for different accuracies of sun-zenith perception. '0° acuity' represents perfect perception of the positions of the sun and the zenith. The dance angles used are from colony 1, Trinidad. Details are shown in Table 5.

What determines whether the turning of the dances is clockwise or anticlockwise when the sun passes too close to the zenith for its azimuth to be perceived? The occurrence of clockwise and anticlockwise turning on the same day at the same place suggests that it is not determined by locality or by clues derived from the very slight changes of sun azimuth that occur during most of the morning and afternoon (Fig. 7). Memorized sun movements from previous days may sometimes have an effect on the more experienced bees. But it seems possible that at least part of the controlling mechanism is of genetic origin. This would make it similar to the mechanism proposed by Kalmus (1956). A genetic effect would explain the behaviour of colony 1, Trinidad, in which for 3 days *all* the dancers were turning in a direction contrary to that expected from sun movement, either on the same day or memorized from previous days. In Jamaica four sets of observations of dances were made on days when the sun was close to the zenith: on one colony while the sun was moving north (1960), two colonies while the sun was moving north (1961), and one colony while the sun was moving south (1961). All four colonies were closely related and all showed a strong bias towards anticlockwise turning of the dances.

Can dances which differ widely from the expected direction be used for communication?

Previous work (New, Burrowes & Edgar, 1961; New, 1961) has suggested that bees can communicate fairly accurate information about the direction of a food-source even when the sun is within one or two degrees of the zenith. The angles of the dances performed at such times deviate so widely from the angles between the azimuths of food source and immediate sun positions that the latter could not possibly be used as a basis for communication. And presumably it is individual dances which are significant for the bees, rather than the means of several dances, because if bees obtained information from the mean of several dances communication of direction would be impossible when the colony was collecting the same food from more than one direction.

However, the extent to which the bees exhibit a systematic turning of their dances, even when it does not correspond with the sun azimuth changes occurring at the same time, suggests that they may be able to use dances to communicate the direction of food-sources without reference to the immediate sun position. The dual mechanism proposed in this paper for control of dance direction would provide a basis for such communication. At times of day when the sun azimuth could be perceived clearly the bees would note its direction relative to the landscape and would orientate their dances accordingly. From these dance angles the appropriate dance angles for other times of day could be 'calculated' by the dual-control mechanism. Thus if the direction of a food-source at time x is communicated by a dance vertically upwards, and at time $x+2$ hr. by a dance y° to the right of the vertical, it could be communicated at $x+1$ hr. by a dance $y^\circ/2$ to the right of the vertical *regardless of the sun position at* $x+1$ *hr.* Communication of direction by dances would still be based ultimately on sun positions relative to the landscape, but not necessarily on the immediate sun position at the time of a particular dance.

To test this possibility the dance angles observed in colony 1, Trinidad, have been used in Fig. 11 as follows. The dances of all 6 days have been combined and the mean deviations calculated, for each 2° interval of sun zenith distance, from the values to be expected if:

(*a*) the dance angles symbolize angles between food-source and immediate sun azimuth;

(*b*) the dance angles are controlled by the dual mechanism suggested in this paper.

On the former assumption the dances appear wildly inaccurate; on the latter, the mean errors are sufficiently small for the dances to be of value in communicating direction even when the sun is within two degrees of the zenith.

The values in curve *b* have been calculated on the assumption that the bees' accuracy of perception of the sun relative to the zenith was 3° during the whole course of the observations. But small changes in this accuracy would cause appreciable changes in the 'correct' dance angles (Fig. 9). Such small changes are likely to occur from hour to hour and day to day as a result of fluctuating weather conditions, and

Table 5 shows evidence of their existence. The bees would all be subject to the same weather conditions and hence could make the appropriate corrections in interpreting the dances. Therefore the values for mean error shown in curve *b* probably only represent the lower limit of accuracy possible.

For communication to be effective bees receiving information must calculate in the same way as bees dancing. The amount of agreement between different dancers provides a measure of the amount of agreement in the colony as a whole. In colony 1, Trinidad, agreement was very good. In Jamaica the behaviour of the dancers was more

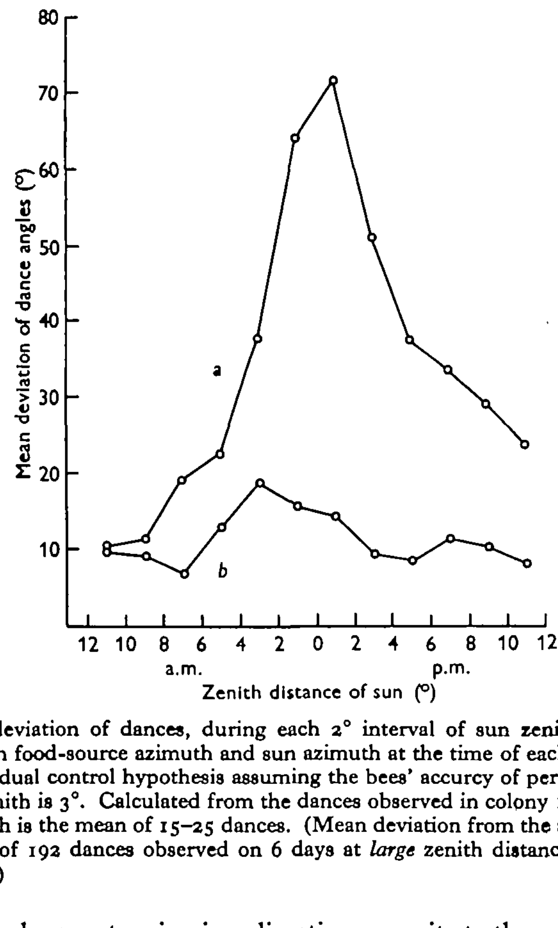

Fig. 11. Mean deviation of dances, during each 2° interval of sun zenith distance, from (*a*) angle between food-source azimuth and sun azimuth at the time of each dance, (*b*) angles predicted by the dual control hypothesis assuming the bees' accurcy of perception of the sun relative to the zenith is 3°. Calculated from the dances observed in colony 1, Trinidad. Each point on the graph is the mean of 15–25 dances. (Mean deviation from the angle between sun and food-source of 192 dances observed on 6 days at *large* zenith distances of the sun was found to be 5·6°.)

varied, some of the dancers turning in a direction opposite to the rest. But even where a colony is divided into 'clockwise bees' and 'anticlockwise bees' useful communication would presumably still be possible between those bees working on the same system.

It is very unlikely that bees will have evolved special mechanisms of communication only for the rare occasions when the sun is close to the zenith. If they can communicate direction at these times then it must be by mechanisms of wider application, the most obvious being mechanisms for use on the frequent occasions when the sun is obscured by cloud. It has already been shown that, provided part of the sky remains clear, the bees can determine the sun position from the pattern of light polarization (von

Frisch, 1948); and provided the cloud layer is thin the sun position can be determined by the distribution of ultraviolet light even in a sky totally covered by cloud (von Frisch, Lindauer & Schmeidler, 1960). The dual-control mechanisms suggested here would make possible directional communication by dances under cloudy conditions of any extent or density.

SUMMARY

1. The dances of honeybees have been studied in Jamaica (18° 00′ N.), Trinidad (10° 38′ N.), and British Guiana (5° 11′ N.) when the sun was near the zenith.

2. When the zenith distance of the sun was less than about 10° the orientation of the observed dances deviated, often very widely, from the direction expected if the bees were indicating the angle between the sun azimuth and the food-source azimuth. But the dance angles did not show the wide scattering to be expected from a failure of perception of sun azimuth. They were frequently well orientated, and successive dances often progressively changed direction clockwise or anticlockwise.

3. The dance angles plotted against time gave smooth curves symmetrical about noon, but of smaller maximum slope than the curves of changing sun azimuth.

4. The direction of turning of the dances was often opposite to that expected from the direction of sun azimuth change.

5. Various conceivable explanations are discussed. It is concluded that the dances can best be explained as the result of two control mechanisms:

(i) A mechanism which uses all available information about the real sun azimuth and limits the possible dance angles to a certain range. This range becomes increasingly wide the nearer the sun approaches to the zenith.

(ii) A mechanism which takes into account the dance directions (or sun positions) memorized for particular times of day, and between successive memorized positions turns the dances through an angle proportional to time. This mechanism is subject to the limits imposed by mechanism (i).

6. This dual-control hypothesis would provide a general explanation of the orientation of honeybee dances. It could explain the orientation of dances at night and when the sky is completely covered with cloud.

7. Evidence is presented that the acuity with which bees can perceive the position of the sun relative to the zenith is not less accurate than 2°–3°. This is a measure of the accuracy with which they can localize a visual stimulus relative to the direction of gravity.

8. The mechanism proposed for orientating the dances would provide a possible means whereby bees might communicate the direction of a food-source by dances which do not indicate the angle between the azimuths of the food-source and the sun.

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