ORIENTATION AND METHODS OF COMMUNICATION OF THE HONEY BEE AND ITS SENSITIVITY TO THE POLARIZATION OF THE LIGHT

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PROBABLY many biologists are by now acquainted with at least the outline of the very remarkable work on the dances of the honey bee published by Prof. K. von Frisch in 1946^{1,2,3}. Since then, two other papers^{4,5} have appeared which have carried the story a great deal further, and it now seems opportune to consider the astonishing picture thus provided of the methods of communication among worker bees and its far-reaching implications as to the capabilities of a bee's sense organs and brain. The zoologist may, indeed, be pardoned if at first he feels sceptical—in spite of the immense detail and thoroughness of the investigation and even though it comes from one of the most eminent living workers in these fields of study. Indeed, one experimental zoologist expressed himself to the writer as almost "passionately unwilling" to accept such conclusions, and "probably many others feel the same—for the implications are certainly revolutionary.

Through the kindness and hospitality of Prof. von Frisch, I was able, during a visit to St. Gilgen, Austria (September 27–29, 1948), to perform with him and for myself at his home at Brunnwinkl (which is also the field station of the Zoological Institute of the University of Graz) 'repeats' of certain of the most crucial experiments. Brunnwinkl is particularly well situated for this work in that commercial bee-keeping is practically non-existent there. It would be difficult, if not impossible, to repeat the work in an area where any hives other than those controlled by the investigator were present. My observations covered all the main phases of the work, and I was able to make my own estimates of the efficiency of the indications of distance and direction of food sources given by the returning foragers to their associates. This memorable experience, for which I owe a great debt of gratitude to Prof. von Frisch, enabled me to resolve to my own satisfaction some of those doubts and difficulties that come to mind on first reading the work, and convinced me of the soundness of the conclusions as a whole.

For the benefit of those who have not read von Frisch's papers of 1946 it may be advisable first to describe the main conclusions. When a worker bee discovers a rich (natural or artificial) source of nectar or pollen, she informs the other inmates of the hive of her find by performing a dance on the comb after her return. Bees which are nearby follow her in the dance, become excited and then apparently fly out to search for the food indicated. Quite early in the work it was noticed that there were two types of dance, the 'round dance' and the 'waggle dance', the latter consisting of a very broad figure-of-eight, during the transverse straight run (the 'waggle run') of which the bee waggles her abdomen from side to side at a constant rate.

If the food source is not more than 50–100 metres from the hive, the round dance is performed. This is merely a signal to the other bees to go out and search around the hive for a food source of the same odour as that adhering to the body of the dancer.

With increasing distance of the food source there is a gradual modification in the type of dance performed, until at more than 100 metres it becomes the characteristic waggle dance. The number of complete waggle dances in a unit of time decreases with increasing distance of the food source. This inverse relationship is so constant that, by timing the dance with the aid of a stop-watch, one can estimate accurately the distance of the food source from which the dancer brings her burden, and it is clear (refs. 1, 2, Fig. 7) that this dance gives an effective and reliable indication to the other bees of distances between 100 metres and 1,500 metres: at 100 metres there being an average of 10 waggle runs per 15 sec., which drops steadily to an average of 4.5 at 1,500 metres. Further observations described in a later paper⁴ show that the waggle dance continues to give an accurate indication of the distance of food source up to 6 kilometres from the hive, the rates at this extreme distance fitting perfectly on to the asymptotic curve obtained for shorter distances. The dance, however, is not effective for recruitment of new bees to a food source beyond 5½ km.

The dancing bee also indicates the *direction* of the food source by means of the waggle dance. It must be borne in mind that these dances are normally performed on the vertical surface of the combs inside the hive. Under these conditions, the direction of the waggle run of the dance indicates the direction of the food source in relation to the position of the sun, which is represented by the vertical direction on the comb. This will be clear from the diagram, no doubt already familiar, on p. 12. Thus we see that a waggle run upwards indicates that the food source lies in the direction of the sun. A waggle run downwards shows that the feeding place is in the opposite direction. A waggle run to the right means that the food source is to be found at the right of the sun and at such an angle to the sun by which the waggle run deviates from the vertical; similarly, a waggle run to the left indicates a feeding place at a corresponding angle to the left of the sun.

Thus the complete waggle dance indicates both direction and distance of a food source, and constitutes for the colony of bees an extraordinarily efficient method of harvesting as rapidly as possible a new and abundant source of food. The dance is only performed when a worker has discovered, or is foraging at, a particularly rich source of supply. Each performance of the dance on the comb results in a number of other bees setting out and finding that particular food source. If the supply is still rich when the newcomers reach it, they also dance on the combs on their return, and so a numerous band of foraging workers is quickly recruited for work at a rich source of supply. As soon as the source begins to fail the returning workers cease to dance, although they themselves continue exploiting that source as long as an appreciable yield is being obtained. The result is that any new source of food is rapidly and fully utilized by the colony without any undue waste of time and energy.

The performance of the waggle dance on the vertical comb is so remarkable that we are forced to ask ourselves whether, apart from human faculties, there is anything comparable known in the animal kingdom; for I think it may be said that the performance of the worker hive bee is essentially an elementary form of map-making and map-reading, a symbolic activity in which the direction of action of gravity is a symbol of the direction of incidence of

Four examples of indication of direction. The sun is to the south-east of the hive. The diagram in each lower left-hand corner shows schematically the direction of the waggle dance for a given position of the feeding place. From *Bulletin of Animal Behaviour*, 1, No. 5, redrawn from *Experientia*, 2, 401 (1946)

the sun's rays. We can assume that the main orienting stimulus when the bee is on the vertical comb inside the dark hive is the pull of gravity on the body, presumably perceived by the proprioceptive sense organs at the limb and abdominal articulations. It is astonishing enough to find that there is an inherent instinctive association of these two stimuli so that one replaces the other according to whether the bee is inside or outside the hive. But this alone does not carry us very far, and we seem forced back to the conclusion that there must be an inherent recognition of the characteristic movement pattern of the waggle run as equivalent inside the hive to the activity of the foraging flight outside it. This is a big assumption, but it seems to be the minimum for any understanding of the problem, for the opportunities which the individual bee can have for perfecting, still less for learning, this astonishing behaviour appear quite insufficient. Thus although correct perception and interpretation of the dance are undoubtedly rewarded by finding the food source, the time available to the short-lived worker bee for improving such an elaborate performance by practice seems altogether inadequate. Moreover, even though a correct interpretation of the dance is rapidly rewarded, by finding food, correct performance of the dance can scarcely be rewarded at all.

There is one particular difficulty which presents itself on first reading of this work, but which I find after observing for myself no longer looms so large. This is the problem of how the bees themselves can observe the characteristics of the waggle dance when it is performed on the crowded surface of the comb

in an absolutely dark hive. It is important to remember that the successful foragers give up some food to the other bees on first returning to the hive. They then do the dance. The bees nearby are excited by the dance and appear to appreciate its direction by following close on the waggle run. They thus experience both the angle and speed of the dance by themselves following the waggle run immediately in the wake of the returning forager.

Von Frisch⁴ has now shown that the direction-giving is, under good conditions, accurate to about 3° , whereas the distance indication is on the average accurate to about 100 m. The accuracy with which the angle between the axis of the waggle run and the vertical is measured by the bee is an astonishing feature of the results, and from our present knowledge of insect proprioceptors it is not easy to imagine how it is achieved. Indeed, the mere visual perception of angles to such accuracy when on foraging flights is very remarkable, for Baumgartner⁶ has shown that the minimum angular separation of adjacent ommatidia in the bee's eye is 0.9° . With regard to distance estimation, it appears, as a result of a large number of experiments on efficiency under varying wind conditions, that this is the result of some sensitiveness to the amount of energy expended on the outward flight. The advantage in estimating the distance on the outward flight is probably that the bee is then unladen and her weight and flight conditions constant.

On the return flight, the load carried will vary according to whether she is foraging for pollen or nectar, and probably with other conditions also; moreover, it is the correct estimate of distance under the wind conditions of the outward flight that matters. The visual estimation of direction, while theoretically simple enough for an animal with good light-compass orientation such as the bee, when foraging in open country without serious obstacles, may nevertheless be a very complex problem under natural conditions, particularly in the broken and mountainous country in which von Frisch's experiments were performed. Bees are somewhat reluctant to fly high over obstacles and tend at first to go round rather than over impediments such as high cliffs and mountain sides; although later, if the detour is excessive, they may quickly learn to straighten the path. Von Frisch, as a result of some preliminary detour experiments, concludes that bees indicate the actual distance flown on the detour but give approximately the true direction of the food source in relation to the sun—not the direction on which they set out. A moment's thought will show that, in fact, this is the simplest way in which direction-giving could be made effective in country where obstacles have to be negotiated.

The waggle dance is occasionally performed on the horizontal surface of the alighting board in front of the hive, and under these conditions the waggle run serves as a pointer indicating the actual direction of the feeding place, not its direction in relation to the sun; for obviously, on a horizontal surface, the type of dance involving reference to gravity is impossible.

A bee performing the vertical form of the waggle dance on the comb in its normal position can immediately be induced to perform the horizontal form by moving the hinged vertical comb of the observation hive to the horizontal position—provided only that a good deal of daylight is being admitted to the hive (in actual fact as long as some blue sky is visible to the bees). In the dark, bees (as observed by a red light to which they are insensitive) are always disorientated when on a horizontal surface or when daylight is too diffuse or reduced below a certain intensity. The primitive function of this horizontal dance is completely obscure. The horizontal alighting board is, of course, entirely unnatural and it is hard to imagine how under natural conditions there could ever be a horizontal surface available for direction-giving.

It is evident that the bees cannot remember the turns which they have taken on the horizontal plane after they have entered the dark hive, and can no longer give the absolute direction unless they are subject to some stimulus received from the daylight, sight of the sun itself not being necessary. If they are given a strong *beam* of light from an electric lamp inside the hive, the straight run of the waggle dance is found to make the same angle with the lamp as the actual path from the hive to the food source makes with the sun, the lamp being reacted to as if it were the sun. But, of course, this is a highly artificial situation. As a result of a long series of experiments, von Frisch found that sight of a very small area (10°) of the blue sky at any point of the compass is sufficient, quite independent of its direction, to maintain correct orientation of the dance on the horizontal surface. If, however, when the aperture is to the north, light from, say, the western side is reflected down the tube into the hive by a mirror, the bees now dance incorrectly, behaving as if west was north. We are thus forced to the conclusion that daylight in itself without sight of the sun has some orienting capacity independent of its direction. A confirmation of this astonishing conclusion was obtained from an entirely different set of observations and experiments, 3,600 in number, planned and carried out in previous years for another purpose (ref. 4, pp. 144–45). Unfortunately, lack of space forbids discussion here of this very impressive evidence.

It appears that the only explanation of all these similar experiments is that the bees are sensitive to the polarization of the light reflected from the blue sky, and by this means are able to tell the direction of the sun even though they can see only a small area of the sky far removed from the sun. The light from the blue sky is partly polarized, and this polarization shows a two-fold relation to the position of the sun; first, the degree of polarization increases as one passes across the sky away from the sun, to reach a maximum of 60–70 per cent at about 90° , declining again towards a point opposite the sun. In a considerable circle around the sun and also around its opposite point the degree of polarization is very slight. Secondly, the plane of polarization of the light from different parts of the sky bears a regular relation to the sun's position. Von Frisch points out that the human eye is slightly sensitive to polarization of light, as is shown by the visual phenomenon known as 'Haidinger's tufts'; and it appears that some individuals have a higher sensitivity than others in this respect⁷. He assumes that compound eyes are particularly well adapted to

analyse polarization of the sky light (although he offers no suggestion as to the means by which this might be done), and that it is perception by the bees of the pattern of polarization thus visible to them in the sky which enables them to determine the actual position of the sun.

Obviously these conclusions pose very considerable problems to those concerned with the physiology of vision in general and the structure of the arthropod eye in particular. Be this as it may, the evidence that polarization of the light from the sky is the effective stimulus is very great. As I myself observed, one can alter the direction of the horizontal waggle dance of the bees by changing the direction of polarization of the light. The effect of placing a 'Polaroid' screen on top of the glass of the observation hive was to change the direction of dancing in the same degree and direction as the turning of the 'Polaroid' screen from the zero point; but when this turn had reached approximately 55° , the bees were completely disorientated and danced at random in all directions. In a series of sixty-two experiments in which the bees were screened from all but a segment of the northern sky 50° broad, 20° high on an average height of 40° above the horizon, it was found that the change of direction of the dance kept pace steadily with the change in orientation of the 'Polaroid' up to 50° . Similarly, if one leaves the 'Polaroid' in one position and changes the screens so that the bees see a different part of the sky, one obtains a corresponding change in direction of the dance (ref. 5, Fig. 10, 1949). A similar change can be induced relative to the movement of the sun if the 'Polaroid' is left in one position (ref. 5, Fig. 11, 1949).

Von Frisch provides strong evidence that whereas under the glass roof of the observation hive light from the blue sky is essential for orientation of the horizontal dance, bees *outside the hive* can still orientate themselves by the polarization of the light even when the whole sky is covered with thin cloud. It seems safe to assume that under these conditions polarization must be greatly reduced, but of the exact extent of this reduction and of the wave-lengths concerned we are given no clue. It is suggested that the additional depolarization caused by the glass cover of the observation hive is sufficient to account for the inability of the bees to orientate their dances on the horizontal comb under cloudy conditions. This is one of a number of points urgently demanding further study and which will, no doubt, be the subject of the present season's work in Prof. von Frisch's Department.

To sum up: while the mechanism of perception of the polarization remains obscure, the essential facts seem to be well established, and it appears that we are justified in the conclusion which von Frisch himself reaches, that the polarization of the light of the sky is an effective indication for bee orientation and possibly for that of other insects also. Thus, outside the hive and on a horizontal surface, the bees can orientate themselves either by landmarks, by the observed position of the sun or by the polarization of light from the sky—or by any of these in combination. Once inside the hive, landmarks are absent; and on a horizontal plane, therefore, they cannot orientate themselves unless they are given one or other of the remaining two stimuli. Presumably, therefore, the horizontal dance can never be done within a normal hive. Once on the vertical comb, however, they get the orientation supplied by gravity, which now 'stands for' the sun, and they

can thus do the vertical form of their dance even in the dark; for they can remember the direction of the food source in relation to the position of the hive and of the sun.

Prof. von Frisch, by his first work on bee behaviour, published in 1922-23, showed the foraging organisation of the hive to be far more complex than had hitherto been conceived. By this latest work (1946-49) he poses tremendous problems for the neurophysiologist and psychologist and shows that the foraging and orientation behaviour of bees is such as to require a reconsideration of some of the most fundamental concepts used in our explanations of the behaviour of insects and other animals. The day of Loeb and the tropism theory now seems far away indeed. In spite of the fact that the honey bee has been closely associated with man for many centuries, it is now clear that we still have a very long way to travel before arriving at anything like a full understanding of its behaviour and social organisation.

¹ Von Frisch, K., *Osterr. Zool. Z.*, 1, 1 (1946).

² Von Frisch, K., *Experientia*, 2, 397 (1946).

³ Von Frisch, K., *Bull. Animal Behaviour*, 1, No. 5, 1 (1947) (translation of ref. 1).

⁴ Von Frisch, K., *Naturwiss.*, 35, 12 and 38 (1948).

⁵ Von Frisch, K., *Experientia*, 5, 142 (1949).

⁶ Baumgartner, H., *Z. vergl. Physiol.*, 7, 56 (1928).

⁷ Boehm, G., *Acta Ophthalmologica*, 18, 109 (1940).

OBITUARIES

Dr. Norman R. Campbell

NORMAN ROBERT CAMPBELL was born in 1880 and was the third son of William Middleton Campbell, of Colgrain, Dumbartonshire. He was educated at Eton and Trinity College, Cambridge. He was a student of Sir J. J. Thomson, became a fellow of Trinity College in 1904, and worked mainly on the 'spontaneous' (as it was then often described) ionization of gases in closed vessels. It is not easy, on reviewing the papers by the various workers in this field, to attribute with certainty the credit for establishing the part played by penetrating radiation in producing ionization, but it is clear that he had correctly diagnosed the cause of the phenomena; and it was in the course of this work that, with A. Wood, he established the radioactivity of potassium. In this period also, in studying discontinuous phenomena, he arrived at 'Campbell's theorem' on the effect of random disturbances on a 'receiving' system.

Campbell was appointed to the Cavendish research fellowship at Leeds, when Sir William Bragg was Cavendish professor of physics there, and he became an honorary fellow of that University in 1913. While at Leeds, he continued to work on the ionization of gases by charged particles, and on secondary radiation, then known as 'delta' rays. Soon after the outbreak of the First World War, he joined the staff of the National Physical Laboratory, and was associated with the late Sir Clifford Paterson in investigating the mechanism of the spark discharge produced by plugs for internal combustion engines, which work was described in a number of confidential reports to the Advisory Committee for Aeronautics.

In 1919 Campbell joined the staff of the research laboratories of The General Electric Co., Ltd., which Paterson had undertaken to organise. As an original member of this staff he took a prominent part in establishing those features necessary to assure free-

dom to the research worker in an industrial organisation; and for many years he was consulted by his colleagues on a wide variety of matters, in which his strikingly original approach was at all times an example and a stimulus.

One characteristic of his scientific work (his willingness to modify conclusions) is illustrated by a series of papers on "The Clean-up of Gases in the Electric Discharge" (published in the *Philosophical Magazine* in the early twenties), though they form only a small fraction of his work between 1919 and 1948. He worked on photo-electric photometry and colour matching, the standardization and theory of photo-electric cells, statistical problems, the adjustment of observations, and (returning, in collaboration with Francis and James, to the theory of random phenomena, the foundations of which he had laid thirty years earlier) the production of 'noise' in thermionic valves and circuits.

In addition to the eighty-eight papers recording this work, Campbell published nine books, of which his "Modern Electrical Theory", "Physics, the Elements" and "Measurement and Calculation" are the most typical of his clarity, his scientific philosophy, and his ability to provoke reconsideration of fundamentals. The acknowledgment, in the preface to his "Physics", to "my masters, Henri Poincaré and Bertrand Russell; but I fear that the latter (at any rate) will think his pupil anything but a credit to him", was entirely characteristic of both the friend and the controversialist. So also was the fact that Campbell undertook the labour of re-writing this large book when the complete original manuscript was lost in the post.

Campbell was a man of the highest principles, and once convinced he was right was uncompromising in his attitude in ethical and scientific discussion. This was apt to lead to controversy—tempered always by readiness to reopen discussions if additional information were provided by his adversary. His chief hobbies were walking and climbing, and he had climbed every Scottish peak over 2,000 ft. He was a delightful companion on these occasions; and he was an excellent host, as those who were fortunate enough to be his guests will well remember.

In 1912 he married Edith Sowerbutts, and they were close companions for nearly forty years; having no children of their own, they adopted a boy and a girl. The last fifteen years of Campbell's life were marred by ill-health, which restricted his physical activities, and he retired in 1944 to their holiday cottage near Lulworth. This was completely destroyed by a bomb later that year, and Mrs. Campbell was severely injured. Ill-health and the loss of their home and nearly all their worldly goods found Campbell still philosophical, logical and unperturbed. The loss of his boy on active service and Mrs. Campbell's death in 1948 he met with great courage, though he was much too deeply attached to them to be unaffected by the loss of their companionship.

Mr. W. Mayhowe Heller

MANY senior members of the British Association, especially those interested in the proceedings and reports of Section L (Educational Science), will learn with regret that one of the first secretaries of the Section, Mr. W. M. Heller, died in Dublin on May 13, at eighty-one years of age. The Section was founded in 1901, with Sir John Gorst, who at