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Communication by Insects: Physiology of Dancing

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The dances which foraging honey bees perform on their return to the hive and which serve to inform their nest mates of the presence of food, its direction, quality, and distance, constitute a pattern of behavior of considerably greater complexity than was once thought possible in insects. Both aspects of this exercise in behavior, namely, the presentation of information and the effective receipt of information, place equally severe demands upon the integrative capacity of the nervous system. A plausible rationalization of the ability to present information, in terms of the known capabilities of the insect nervous system, and a possible explanation of the origin of this ability are suggested by a series of observations of the responses of flies (*Phormia regina*) following stimulation by sugar (*1*).

Behavior of Flies

The pattern of locomotion which a crawling fly displays on a horizontal surface under uniform lighting varies according to the exteroceptive stimuli encountered. For purposes of the present discussion, three conditions may be recognized: (i) the absence of specific stimuli; (ii) the continuous presence of stimuli; (iii) the withdrawal of stimuli. When it is placed in the first situation, a fly tends to travel in a series of short (approximately 25 centimeters) straight lines connected in a random fashion as far as general direction is concerned. The second situation is exemplified by the actions of a fly which, in the course of its running, suddenly encounters with its tarsi a drop of sugar. The fly immediately halts and turns toward the point source of stimulation so that the mouth parts are brought over the spot. The proboscis is extended, and feeding commences. The fly remains in this position as long as the mouth parts are adequately stimulated. Thus, the characteristic locomotory response to continuous uniform stimulation is complete cessation of movement.

When walking on a paper evenly painted with a sugar solution, the fly adopts an irregular circuitous path (Fig. 1). This situation does not actually constitute continuous stimulation because, although the tarsal receptors are indeed constantly stimulated, the mouth parts are not. The tracks depicted in Fig. 1 represent mouth prints indicating where the fly sucked until stimulation ceased, whereupon locomotion was resumed. Therefore, this situation in fact represents typical behavior exhibited upon withdrawal of stimulation. In short, if the source of dominant stimulation is removed before the fly has fed to repletion or is removed as a result of the fly's having consumed it completely, the fly begins what, to all intents and purposes, appears as a purposeful searching action.

This action is most clearly seen in the case in which a fly is momentarily presented with a single drop of sugar. The response takes the form of repeated clockwise and counterclockwise turnings in the area of the former drop (Fig. 2). That the action is completely stereotyped, rather than purposeful, is demonstrated by the fact that a fly which is held in the hand and stimulated with sugar, immediately upon being released on a horizontal surface, begins "searching" actions on the spot with no relation to the spatial location of the former stimulus. The action is purely automatic. Two features of this behavior are worthy of particular notice: (i) it takes place *after* the stimulus is removed and continues for some period of time; and (ii) it strikingly resembles a dance.

The intensity and duration of the response is modified by three variables: the concentration of the stimulus; the threshold of the central nervous system of the fly; and the time lapse between the withdrawal of stimulation and the onset of response.

For example, after stimulation with 0.1-molar glucose, there are few turnings, of short duration, before the fly resumes its former random-like mode of running (Fig. 3). After stimulation with 0.5-molar glucose, the fly exhibits a more convoluted action of longer duration. After stimulation with 1.0-molar glucose, there is still greater convolution and longer persistence of action. These actions differ, not in the acuteness—that is, degrees—of angles of turning, but in the number of turns per unit time and the total duration of action. The concentration with which the fly had been stimulated can clearly be predicted from the pattern of subsequent action.

For any given concentration of stimulus, the intensity and duration of response is related to the threshold of the central nervous system, and any change in the physiological state of the fly which alters this threshold is reflected as a change of response. The nutritional state of the fly thus affects taste acceptance thresholds (*2, 3*). A starved fly performs more active gyrations in response to 0.1-molar glucose than a fly which has recently fed. Flying also affects threshold. A fly which has flown for an hour, for example, responds more actively than one which has flown for only 10 minutes.

The importance of the third variable, time, with respect to the intensity of response is related to the decay in intensity. In other words, the rate of turning gradually diminishes as the action proceeds until there is complete cessation

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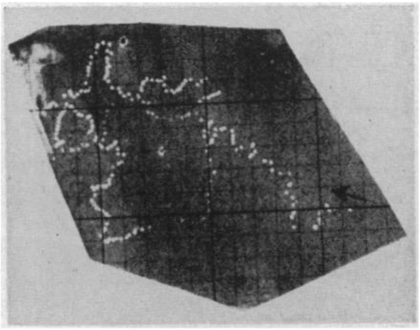

Fig. 1. Pattern of locomotion of a fly on a surface painted with a sucrose solution containing methylene blue. Each white spot represents a point where the labellum was appressed to the surface and the solution was sucked up completely.

and the fly resumes its random movements. Accordingly, any isolated segment of the action characteristically represents the elapsed time between the end of stimulation and the beginning of the particular segment. Since the rate of turning diminishes with time, a diffuse segment of the pattern represents a long time lapse, and a tightly convoluted segment represents a short time lapse. Furthermore, the longer a fly is prevented from responding after stimulation (by being held in the hand, for example), the less intense is the response.

If, at any time during the response, the fly is subjected to the continuing influence of some directional stimulus, such as light, the response acquires a directional component. The pattern of action becomes deformed by being elongated in a plane parallel to the beam of light (Fig. 4). In the dark the pattern is formless. If the fly is permitted to perform its gyrations on a vertical surface in darkness, in which case the continuing directional stimulus is gravity, the action acquires a directional component. The path is elongated parallel to the vertical axis. Light shining on the vertical surface destroys the directional component of the pattern (Fig. 5).

Resemblance to Bee Dances

At this point it is clear that there are some striking parallelisms between the gyrations of the fly and the communicative dances of honey bees. With the fly, the intensity of reaction—that is, the number of turns per unit time—and the duration of the dance are related to the concentration of the initiating stimulus; with the bee, the vigor of the waggle dance and its duration are related to the concentrations of the nectar collected. With the fly, the rate of turning diminishes with time after stimulation so that, with a constant stimulus, any given elapsed time is reflected as circling of given intensity; with the bee, the number of turns per unit time is related to the distance of the food from the hive, that is, flying time (but see subsequent paragraphs)—the greater the distance, the fewer the turns and the more diffuse the dance. With the fly, a continuing stimulus in the form of light or gravity imparts some direction to an otherwise disoriented action; with the bee, the orientation of the dance is related to the direction of light or polarized light when carried out on a horizontal plane and with gravity when conducted on a vertical plane in darkness. If the bee performs its dance on a horizontal comb in darkness, the dance is disoriented; that is, the successive runs point in different directions. The dance also becomes disoriented if light shines on the bee while it is dancing on a vertical comb.

Two major points of dissimilarity in the behavior of the two insects are immediately apparent: the gyrations of the fly possess intensity and direction but lack the clean geometric pattern so characteristic of the bee's waggle dance; the gyrations of the fly lack the precise angular orientation which is one of the main features of the bee's waggle dance. With regard to the first point, there is one important respect in which the circumstances of dancing bees generally differ from those of the circling flies—namely, the crowded conditions under which the bee usually dances. To simulate crowded conditions, a stimulated fly was forced in one experiment to perform in the midst of a crowd of other flies. Under these conditions the action lost some of its diffuse character and acquired a crude geometry of pattern. Furthermore, an insect with short antennae which do not reach the ground makes up for its inability to palpate by crawling in wide, irregular paths. An insect such as the wasp *Polistes,* which palpates the ground with its antennae, can be made to perform a much neater dance than the fly.

With regard to the second point, it must be admitted that the fly cannot be induced to circle at any particular angle with respect to either light or gravity. The difference between the two insects may possibly be accounted for in terms of the highly developed light-compass reaction of the bee and its comparative unimportance in the life of the fly. In its normal relations with the environment, the honey bee relies heavily on a light-compass reaction for orientation at a distance, whereas the fly, although capable of some degree of light-compass response, is largely restricted to positive and negative phototaxis. In each insect, the behavior with respect to light has its counterpart in the effect of light on the orientation of the dance. In this connection it is pertinent to recall that Vowles (*4*) had postulated one taxis mechanism common to distance orientation to the sun, plane of polarization of light, and gravity and another taxis mechanism operating for orientation to near objects. Vowles regarded the first as the primary mechanism, and Thorpe

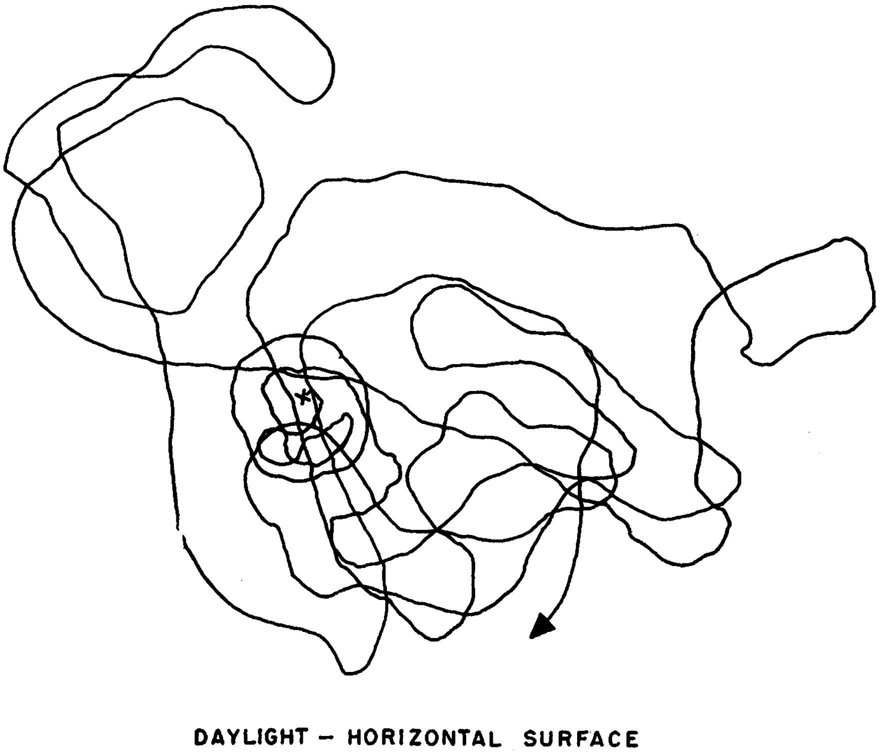

Fig. 2. Pattern of locomotion performed in daylight on a horizontal surface by a fly which has been stimulated briefly with sucrose.

(*5*) indicated that the primary mechanism is innate and the other mechanism learned. The observations on the effect of light and gravity in the gyrations of the fly support these conclusions.

The comparison between bee and fly behavior may be carried one step further. When the foraging bee returns to the hive, it regurgitates nectar which is accepted by other bees. The forager then begins dancing, and as it dances its way among the crowd, other bees become excited to the point of following the dancer. When a fly which has recently been fed is placed in a crowd of unfed flies, it cleans its appendages and almost invariably regurgitates some of its crop load. Surrounding flies become greatly excited, follow the fed fly around, attempt to lick sugar from its mouth parts, and even begin gyrations of their own which are indistinguishable from those performed by the first fly. The superficial resemblance of this performance to that of bees dancing in the hive is striking.

Furthermore, if the first fly is fed with a sugar solution containing methylene blue, it is possible, a few minutes later, to detect the dye in the guts of many of the other flies. Clearly, both the fed fly and the foraging honey bee normally regurgitate; the bee disgorges nearly completely the contents of her crop; the fly only a fraction. The comparison suggests that the highly developed trophallaxis, or food-sharing, which goes so far in unifying the bee colony evolved from rather basic and simple individual behavior of the type exhibited by the fly.

It is not possible in the present context to carry the comparison of the two species further. The fly, being solitary rather than social, apparently does not act upon the information contained in the circling performance, beyond being excited enough to follow the circling individual until it flies away. The culminating act of the bee's dance—that is, the departure of stimulated members of the audience for the field—does not follow on the part of the flies. The stimulated flies do not go anywhere, nor would this final step logically be expected.

The circling response of the fly is a facet of adaptive behavior which serves as an effective pattern for food-searching. Since there are contained in it many of the basic components which characterize the waggle dance of honey bees, the possibility exists that the dance of the honey bee might have been derived from a primitive and basic behavior pattern of this sort. The many resemblances suggest this interpretation. This idea is also favored by the fact that there are dance patterns of various degrees of complexity from one species of bee to the next, and within a given species. For example, the Western honey bee, *Apis mellifera,* performs a wide variety of dances, ranging from formless gyrations to the highly stylized waggle dance (*6, 7*), and bees fed *inside* the hive run about excitedly but fail to perform an organized dance. Other species of bees, as, for example, *Apis florea,* perform dances of lesser degrees of complexity (*8*).

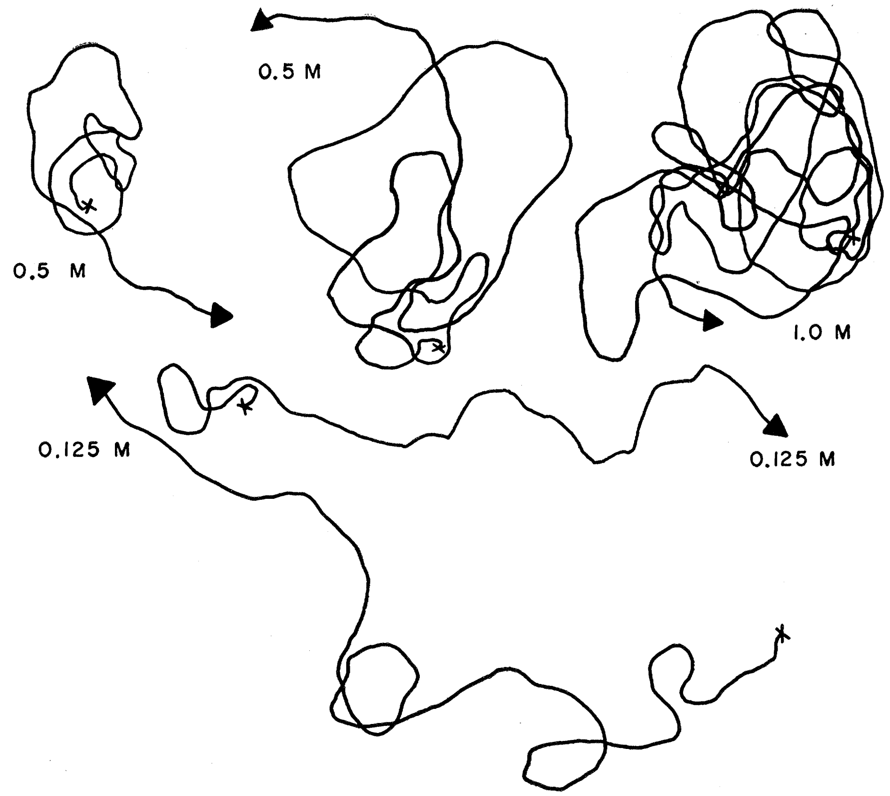

Fig. 3. Variations produced in the pattern of poststimulatory locomotion when the concentration of the stimulus is changed.

Relation of Dance to Stimulus and Response

The striking manner in which a fly's behavior can be described in terms of stimulus and response suggests the possibility of interpreting the waggle dance of the honey bee in similar terms. Although any attempt at complete interpretation at this time would suffer from gross oversimplification, a working hypothesis can be proposed which may direct further investigation into profitable channels. The hypothesis may be stated in the following terms: the waggle dance is a delayed response to effective taste stimulation and is regulated by a central nervous system threshold. It must be pointed out at the start that, while the hypothesis in its present form can explain many of the characteristics of honey bee dancing, it cannot explain all.

As von Frisch (*9*) proved, the waggle dance is coded to impart the following information: distance of food source from the hive, direction of food source from hive, and quantity and quality of food. The nature of the food is indicated by the odor of the flower of origin, this odor adhering to the bodies of foragers and being contained in the nectar. This fact need not concern us here. Direction is indicated by the orientation of the dance axis with respect to light or gravity and, likewise, falls outside the scope of the present discussion.

The remaining data are coded principally as intensity of dance—that is, number of turns per unit time. They are also coded as duration of dancing. The code has certain ambiguities in that quantity, concentration, and distance may be signified by the same means, vigor and duration of dancing (*9*, pp. 113, 118). On the basis of this code *alone,* bees should be unable to distinguish between concentrated sugar at a distance and dilute sugar near at hand. That such is actually the case has recently been demonstrated by Boch (*10*). This state of affairs would truly represent an unfit adaptation for survival were it not for the fact that there is a safety factor in the form of a duplicate code. Distance of supply is also indicated by the site of dancing within the hive (*10*). For short distances, the dance is performed near the exit hole; for long distances, at a more remote position in the hive. In addition, the number of bees dancing also indicates distance, quality, and quantity. There may be other factors as yet unknown. The ambiguity strongly suggests that the critical factor or stimulus regulating the dance is identical for the three parameters distance, quality, and quantity.

A clue to the nature of the controlling stimulus is given by an early observation of von Frisch—namely, that adulteration of the food in the field has a pronounced effect on the character of the dance. This finding points to taste as a controlling stimulus. The foraging honey bee on a round trip from hive to food is stimulated at least three times. Before departure the bee imbibes honey, in the course of which its oral organs of taste are stimulated; while collecting nectar, the bee is intermittently stimulated as it visits successively different blossoms; upon return to the hive, the bee disgorges its load and is stimulated for a third time.

There is one other possibility which cannot be overlooked. The presence of sugar in the fly's fore-gut, or mid-gut, or both has a pronounced effect on the taste threshold, most likely through mediation of receptors in the gut, since the crop seems to play no role (*3*). It is conceivable that a similar situation prevails in the honey bee, in which case stimulation could be effected without the oral organs of taste being stimulated.

If the dance is a delayed response to a taste stimulus, at which of the four moments of stimulation is control over the dance established? It might be argued that the first (fueling) and second (food-gathering) stimuli are too far removed in time to be effective. However, experiments with the fly overcome this objection. For both the bee and the fly the duration of the dance is the same, from a few seconds to 1 minute. For the bee, however, the elapsed time between stimulation at the site of food collection, for example (if this is indeed the moment of stimulation which is critical), is occupied by flying. In other words, another behavior pattern, flying, is interposed between stimulation and dancing. Since bees fly about 14 miles per hour and the maximum extent of foraging is usually 3 miles, the maximum duration of interpolated flight is from 15 to 20 minutes.

Can flying temporarily inhibit dancing? In the case of the fly, it has been demonstrated that a fly which is stimulated with glucose and forced to fly immediately thereafter will, upon the moment of landing, begin the circling which has been delayed by flight. Delays as long as 5 minutes have been recorded. If no flying is interpolated, the maximum delay before extinction of the response is of the order of 1 minute. Thus the possibility of the critical stimulation occurring at the time of fueling or collecting is theoretically tenable.

It is unlikely on other grounds that stimulation at fueling is a factor. Although the quantity of honey taken on as fuel is said to vary according to the distance to be flown (*11*), the concentration is constant, as compared with the concentration of nectar picked up in the field. Since there is a relation between the tempo of the dance and concentration, the importance of fueling tends to be ruled out. Furthermore, von Frisch's observation that adulteration in the field affects the dance tends to eliminate fueling from consideration.

Evidence that regurgitation may be concerned in releasing the dance is implied by the fact that a forager in the hive disgorges a bit, dances for a few seconds, stops, moves away, disgorges again, then again dances. So it is clear that dancing may occur after several regurgitations. On the other hand, the report that bees sometimes dance on the landing board before regurgitating indicates that regurgitation is not invariably essential for dancing. In any event, there are ample opportunities for a taste stimulus to operate, and the time of stimulation, whether in the field while collecting, in flight through the mediation of internal receptors, or in the hive while disgorging the load, is not crucial to the hypothesis, since any of these eventualities can be accepted.

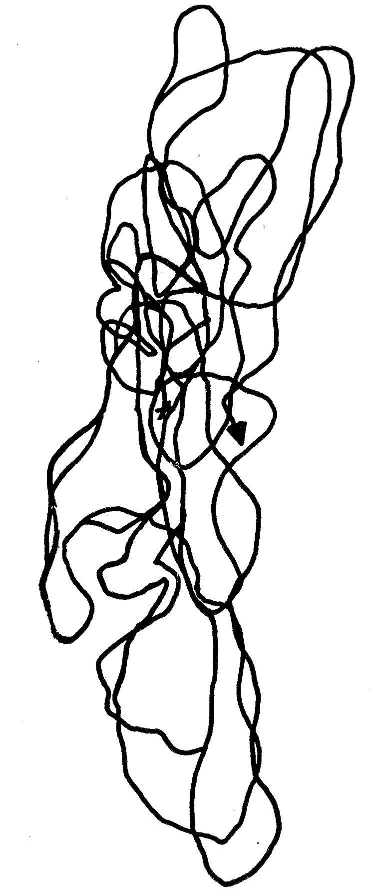

Fig. 4. Pattern of locomotion performed by a fly which is allowed to crawl on a horizontal surface in a beam of light after having been stimulated briefly with sucrose.

What is critical is the idea that the *intensity* of the stimulus is limiting. By intensity is meant, not the absolute concentration, but the concentration in relation to threshold. As the behavioral or central nervous system threshold changes, so does the dance of the fly change. Accordingly, for any given concentration of stimulus, if the taste threshold is high, the dance will be slow; if the threshold is low, the dance will be fast. Therefore, any factors which affect threshold may be expected to affect the dance. Two such factors are hunger and flight. Again in the case of the fly, experiments in our laboratory have shown that taste threshold drops in a regular fashion as flying time increases. The longer the flight, the lower the threshold.

The bee does not differ qualitatively in these respects. Direct measurements of the taste thresholds of individual bees have revealed that the tarsal, antennal, and oral thresholds decrease as the bee is starved (*3*). In our experiments the threshold of the bee had fallen to its lowest level about 60 hours after feeding to repletion with 2-molar sucrose. At this time the crop was nearly empty. The same striking drop in threshold could be brought about by flying the bee continuously for about 1½ hours. In each case renewed feeding was followed by a rise in threshold in excess of 30-fold.

Energy Expended in Flight

There are compelling reasons for believing that the critical variable regulating the intensity of the honey bee dance is energy expenditure (*12*). The work with flies demonstrates convincingly that there is a relation between energy expenditure and threshold. This is indicated by the fact that threshold decreases less rapidly as a fly is flown at low temperatures than when it is flown at high ones. Since wing-beat frequency and energy expenditure are greater at higher temperatures, the drop in threshold is clearly related to this factor rather than duration alone. But just what is mean by energy expenditure and just what relation does exist between this factor and threshold are still unclear. Several possibilities have been eliminated experimentally in the fly's case. Blood sugar level, glycogen level, and crop distention are not concerned (3). Present evidence suggests more strongly that some receptor mechanism within the gut is affected by the dynamic relation between the rate of utilization of carbohydrate and the quantity supplied. Similar experiments with the bee give no indication that this insect behaves any differently.

If, as seems to be the case, energy expenditure is the critical determinant for the dance, in which segment of the round-trip flight is the code laid down? Almost all workers agree that the distance which is coded is that of the outgoing flight. Khalifman (13) holds the opposite view that the return flight is critical. There is, however, an abundance of evidence to support the first view, and the adaptive value of the dance really requires that the characteristics of the outgoing flight be read from the dance. For example, von Frisch found that bees flying out against a headwind, and home with an assisting tailwind, indicate in their dances the outgoing distance. Heran (12) has shown that bees flying uphill on the outgoing flight and downhill on the return flight indicate the conditions of the outgoing flight.

The variables experienced in flight which affect the characteristics of the dance are duration, wind velocity and direction, grade of flight with respect to the horizontal, air temperature, and velocity of flight (12). These are reflected in the dance as follows: short distance, short duration, tailwind on outgoing flight, downhill outgoing flight, low temperature, and low velocity all cause the dance to be more intense (faster) and longer; long distance, long duration, headwind going out, uphill going out, high temperature, and high velocity all cause the dance to be less intense (slower). Heran (12) has concluded that the indicated distance is coded through energy expended on the outgoing flight.

All attempts to understand the mechanisms of coding have been confounded by the fact that the dance correctly indicates the conditions of the outgoing flight. While Heran (12) clearly states that the hypothesis that the indicated distance is coded through expenditure of energy on home flights cannot be maintained, and further points out that the exact meaning and measurement of energy expenditure by the bee is uncritical, the role of the home flight should not yet be completely ruled out of the picture.

The hypothesis of control by taste threshold offers an explanation which merits further exploration. It is possible that the dance is regulated *inversely* by events experienced on the homeward flight. For example, if the bee flies out against a headwind, it will return with a favoring tailwind. The energy expended on the return trip will be comparatively small, the taste threshold will remain high, the nectar collected will not constitute a very intense stimulus. Since the intensity of stimulation is a factor which can regulate dancing, the dance will be slow. Slowness indicates a long flight out, which in this instance is indeed the case. Conversely, if the bee flies out with a favoring tailwind, it must return against a headwind; the expenditure of energy will be greater; the threshold will be correspondingly low; the dance will be fast, which indicates a short flight out and is indeed the case. For headwind and tailwind one may substitute uphill and downhill, high flight velocity and low flight velocity, and the relation of these factors to dancing is similarly explained, since all affect threshold in identical fashion.

As attractive as this hypothesis may be, however, it fails to explain situations in which the outgoing and incoming flights are of equal duration and effort. It is clearly an oversimplification, yet it does contain some features that fit the known facts, and further experimentation on energy threshold relationships might be profitable.

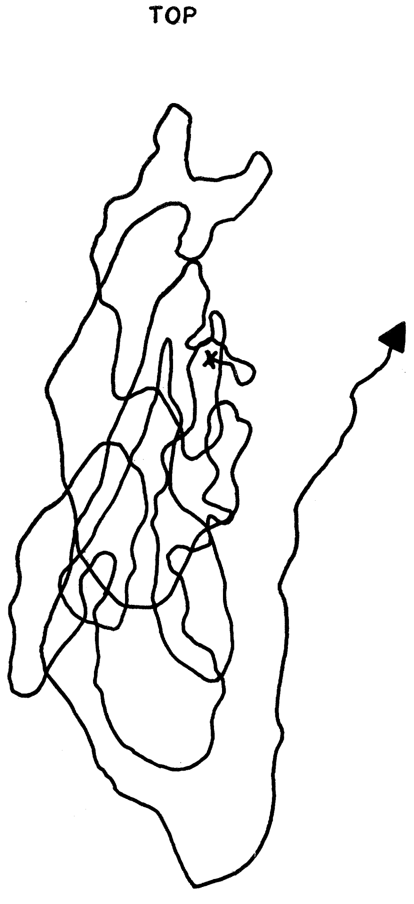

Fig. 5. Pattern of locomotion performed by a fly on a vertical surface in darkness after brief stimulation with sucrose.

Hypothesis Based on Proprioception

The only other major detailed hypothesis which has been proposed is that of Ribbands (14). It envisions the duration and intensity of stimulation of antennal proprioceptors by wind as regulating the dance rhythm. Heran (12), in studying the effect of wind velocity on dance characteristics, investigated this idea. Employing fixed bees, he found that the amplitude of wing beat decreased with increased wind velocity unless the antennae were amputated or fastened, in which case the change was smaller. From experiments of this sort he drew the conclusion that wind velocity was perceived by the antennae, that duration and intensity of wind faced provided a measurement of the distance flown, and that the dance shows a distance based on the duration and intensity of the air stream perceived on the outgoing flight.

But while it is true that proprioceptive information of the sort described is perceived through the antennae and that interference with antennal receptors prohibits compensatory regulations of flight, it does not follow that there is a causal relation between antennal proprioception and dancing. In other words, differences in velocity and the attending differences in flight characteristics mediated through antennal receptors assuredly affect the energy expenditure of the bee and presumably its threshold. Were it possible to remove the antennae without affecting flight, it is doubtful that the absence of proprioceptive input alone would alter the characteristics of the dance. The great difficulty in all conceptions which visualize stimuli experienced on the outgoing flight as having a direct influence on dancing is that the same stimuli experienced on the return flight must be ignored or subordinated.

Importance of the Physiology of the Individual

No pretense can be made of explaining fully the physiology of the dances of honey bees in terms of the performance of flies. Yet the fact that a type of fly behavior resembling bee dancing can be described in terms of stimulus and response offers a basis for removing the phenomenon of bee dancing from the realm of mysticism and for explaining it in physiological terms. There seems to be adequate reason for believing that the communicative dance of bees represents a highly evolved form of primitive search pattern which is innate and stereotyped. There are many dances of bees, such as some of the transitional dances and dances signifying food close at hand [for example, the "pull dances" described by Hein (*6*) and the "sickle dances" described by Lindauer (*15*)], which are less stylized and uniform than the more widely publicized figure-of-eight waggle dances. Thus there appear to be all gradations between excited gyrations and organized dances in the Western honey bee, and from one species of bee to the next. It is not unreasonable to expect that these locomotory responses would be casually related to stimulation by food substances. Since taste threshold is clearly related to energy expended, taste stimulation offers a unique mechanism for a sensory measurement of expenditure.

Because the honey bee is a member of a complexly organized society there is frequently a tendency to regard it as a unit whose actions are subordinated to the needs of that society. Inherent in this view is the danger of considering the insect society as a superorganism (and indeed this view has at times been expressed in the classical literature) and, more dangerous still, of overlooking the physiology of the individuals which constitute the society. The point is well illustrated by the mode of thinking which treats the crop or honey sac of the honey bee as community property which the bee dutifully fills in the field and as dutifully empties in the hive. The fact of the matter is that the crop of the honey bee is as much its own as that of the blowfly is its own. In both insects it is a place of storage, since both insects gorge themselves to repletion upon finding food. Both species use the contents of the crop freely for their own requirements. As postingestion time lengthens, the contents of the crop are directed to the mid-gut for the individual's own metabolism, and as the insects fly the contents are used as fuel. In both species there is a tendency to regurgitate when the crop is full.

In many respects, if the physiology and behavior of the individual are considered, much of colonial life seems to have its basis in stereotyped aspects of behavior which are seen to be fully developed in solitary insects but which have been adapted for the special needs of colonial life and for cohesiveness of the colony. But the physiological requirements and behavior patterns of the individual are not thereby abrogated. The parallelism between the "dancing" of the fly and the dancing of the honey bee is a case in point. The fly and the bee alike are moved to dance by an innate response to a taste stimulus. In both insects the intensity of the taste stimulus is modified by the individual's nutritional state (*16*).

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Useful Application of Bronsted Catalysis Law

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In several studies on the reaction between isopropyl methyl phosphonofluoridate (Sarin) and nucleophilic agents where these agents have been the anions of families of weak acids such as the catechols (*1*), hydroxamic acids (*2*), and oximes (*3*), it has been observed that, within each family of weak acids, a linear free-energy relationship of the Bronsted type (*4, 4a*)

$$k = G_B K_B{}^{\beta} = G_B \left(\frac{K_W}{K_A}\right)^{\beta} \qquad (1)$$

exists between the rate of reaction and the ionization constant. In each case, the reaction was kinetically of the second order and was found to fit the following equation.

$$\frac{dx}{dt} = k\,[\text{Sarin}]\,[\text{anion}] \qquad (2)$$

In this reaction, 1 mole (or in some cases 2) of nucleophilic agent was consumed per mole of Sarin. However, if the nucleophile was maintained in large excess over the Sarin, the observed rate of the over-all reaction was first order, with the rate directly related to the concentration of anion. Under these conditions, the rate constant, $k_{\text{obs.}}$, is defined by

$$k_{\text{obs.}} = k\,[\text{anion}] \qquad (3)$$

Epstein, Rosenblatt, and Demek (*1*) have shown, in connection with their study of the rates of reaction between various catechols and Sarin, that, in aqueous solution under conditions of fixed *p*H and total concentration of reactant (anion plus free acid) for a series of compounds which exhibit a Bronsted relationship, there exists a very rapid reactant. The dissociation constant of this member of the series can be calculated by differentiating the observed rate constant with respect to the basic dissociation constant, K_B, of the reacting anion.

A relationship of this type, when applicable, can be of considerable practical value in the development of "best" reagents where rapidity of reaction is important, as for example in decontamination, detection, certain chemotherapeutic applications, and in analytic procedures. Thus, once the Bronsted relationship has been found to apply on the basis of a limited sampling (as indicated by a linear relationship between log *k* and pK_A), it is possible to predict which

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