Sound: An Element Common to Communication of Stingless Bees and to Dances of the Honey Bee

Abstract. *Sounds are an important part of the communication behavior, the so-called dances, of the honey bee. Stingless bees, which do not use dances for communication, use sound signals to indicate the existence and, in some cases, the distance of a feeding place. The social organization of communities of stingless bees is more primitive than that of honey bees, yet certain common features of communication behavior in these two groups lead to a new hypothesis of the evolution of dancing behavior of the honey bee.*

Karl von Frisch discovered the meaning of the dancing behavior of the honey bee (*1*). A successful foraging bee informs its hive-mates through its dance of the direction, distance, and quality of the feeding place from which it has returned. Within the family of bees, only the four species of the genus *Apis* (*2*) perform this kind of dance. Since there is so little variation in the dancing behavior of these four species, it is difficult to obtain evidence of phylogeny from studies of this dancing behavior. Recent work (*3–5*) has shown that sound production is also important in the communication behavior of *Apis*. Since sound production is found in more genera of the bee family than is dancing behavior, it seems to furnish a means of tracing the evolution of "bee language."

The experiments described in this report, which lead to a hypothesis concerning the evolutionary development of "bee language," were carried out in Rio Claro, Brazil, with stingless bees of the genera *Melipona* and *Trigona*.

The bees were kept in observation hives (*2*) and were trained to visit artificial feeding places at different distances from the hive (0 to 700 m). When the feeding solution was of high quality (2*M* cane sugar), the foraging bees started to "sing" as they entered their hives. We recorded these sounds on tape by means of a special microphone and analyzed them, using methods described previously (*3*).

Foraging bees of *Melipona quadrifasciata* Latr. and *Melipona (seminigra) merillae* produced sound impulses. The frequency during each impulse increased from 300 to 600 cy/sec with the environmental temperature of the hive. The time between two sound impulses was practically constant for all distances at which food was placed, but the length of each single sound period was strongly correlated with the distance of the feeding place from which the "singing" bee had returned. It increased from 0.4 second, if the feeding place was near the hive, to 1.5 seconds if the feeding place was 700 m away. These results are shown in Fig. 1 which also shows the time needed for one sound-marked "waggle" run of *Apis mellifera* at the same distances. Our observations indicate that in both *Apis* and *Melipona*: (i) a distance-dependent signal is given by a foraging bee in the hive, and (ii) this signal is understood by the hive-mates, as indicated by their search for the announced feeding place at the right distance.

We have also detected a similarity in the method of announcing the direction of the feeding place. At the entrance to the hive was a plastic tube, 20 cm long, through which we could see which bees intended to leave the hive. If a foraging bee returned and informed its hive-mates that there was food to be obtained, the hive-mates usually ran to the entrance of the hive in time to follow the foraging bee during the first part of another flight. In *M. quadrifasciata*, we observed that this departure of a foraging bee is marked by a zigzag flight leading to a height of 5 to 10 m, but the followers soon lose contact with the guiding bee and return to the hive. There they wait for the next flight of "their" collecting bee (which is most probably recognized by sound and smell). This behavior would be repeated many times until suddenly another worker bee would fly by itself to the announced feeding place. This behavior could easily be observed on cold winter days (15° to 20°C) with the feeding place 300 m away. On such days all bees leaving the hive would be part of our experiment, and we could train a single collecting bee. This bee had to visit the feeding station 20 to 30 times before the first worker bee arrived. Since the latter often arrived when the foraging bee was still in the hive, it must have found the way by itself.

In another experiment, bees from a hive of *M. quadrifasciata* were trained to visit a feeding station about 10 m from the hive. All bees were marked, and then food was removed until the bees no longer visited the feeding place. As soon as the signal for a nearby (0 to 30 m) feeding station was played from the tape recorder through a loudspeaker connected to the hive, old and new bees arrived at the 10-meter feeding place [this result is similar to that obtained by Lindauer and Kerr with a different arrangement (*2*)]. The bees did not respond to a signal for a feeding station 300 m away or for a station at any other distance.

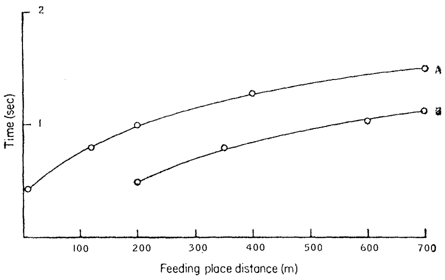

Fig. 1. The correlation between the distance of the hive from the feeding place and the length of each particular sound signal in (*A*) *Melipona quadrifasciata* and (*B*) *Apis mellifera.*

This experiment was repeated with the playing of a recording for a feeding station placed 300 m away. Neither this recording nor recordings for any other distance would induce the bees to leave the hive. The only effect we noticed was that, when the sound was played back, the number of bees that ran to the entrance of the hive increased remarkably. It is possible that the other worker bees missed the information about the direction and the bees trained to fly to the 300-m station missed the smell of the feeding place. If the experiment was repeated with both sound and smell being provided, the trained bees would fly to the 300-m station. Although it was difficult to decide whether sound or smell was more effective, smell alone appeared to be a sufficient stimulus for the trained bees to fly to the 300-m feeding station.

All bees of the genus *Trigona* tested in our experiments, *T. (Scaptotrigona) postica*, *T. (Axestotrigona) tescorum*, *T. (Partamona) cupira*, and *T. (Friseomelitta) varia*, produced sound signals when returning from a successful collecting flight. The analysis of this sound did not reveal any correlation between the sound and the distance of the feeding place. This is consistent with the behavior of these bees. None of the hive-mates tested had any information about the position of the feeding place (*2*). All of them searched for food at all distances and in all directions from the hive, except *T.* (*Scaptotrigona*) *pos-*

tica. The latter marked the way from the feeding place to the hive with scent marks, and the foraging bee guided its hive-mates along these marks to the feeding station (2). With *T. (Axestotrigona) tescorum* we observed that the returning bees stimulated their hive-mates to "sing." In a short time, sound was made by most of the hive members, who then left the hive in great numbers to search for food. The sound record of this event, when played back into the hive later, did not stimulate the singing behavior but did increase the number of bees leaving the hive. With all other *Trigona*, the playing back of the authentic sound increased only the number of bees which ran to the hive entrance, but not the number actually leaving. It may be that smell is an important factor in the communication of these bees.

In the course of our experiments we trained individuals of *Bombus atratus* to visit artificial feeding places. No foraging bee of *Bombus* produced a characteristic sound signal upon returning to the hive, nor did any bee bring another worker bee to the feeding station. *Bombus* obviously cannot communicate information about feeding stations.

These results enable us to form a new hypothesis of evolutionary development of communication behavior concerning distance and direction of food sources. Sound is an element of communication which is widespread in the family of bees. The duration of single sound periods gives the distance of a feeding place in some species of stingless bees and in the honey bee. Stingless bees do not dance. These more primitive bees guide the hive-mates personally to the feeding place by tracing of odor or by repeated indication of flight direction. This personal guiding is symbolized in the dances of the more highly evolved genus *Apis* by the waggle run (5), which forms the main part of the dance in which both distance and direction of the feeding place are indicated.

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Evoked Brain Potential Correlates of Psychophysical Responses: Heterochromatic Flicker Photometry

Abstract. *The relation between the amplitude of evoked brain potentials in man and the relative luminance of two flicker components of different color was determined. The function, which is U-shaped, has a minimum which occurs near the point of equal luminance as judged by the psychophysical method of flicker photometry.*

The data from many studies of human brain potentials evoked by visual stimuli show that various parameters of the response are correlated with the physical parameters of the light stimulus. For example, numerous studies have shown that the amplitude of the evoked brain potential is a function of the luminance of the stimulus (1). Some investigators have attempted to ascertain the relation between the electroretinogram amplitude-luminance function and the evoked brain potential amplitude-luminance function to flickering stimuli (2). Only one previous study has attempted to directly compare simultaneously obtained psychophysical estimates with evoked brain potential measures of responses to flickering visual stimuli (3).

We have investigated the relation between the evoked brain potential and luminance, as measured by a version of the psychophysical method of heterochromatic flicker photometry. With this method of visual photometry, a flash of colored light typically occupies one half of a cycle and a flash of a standard reference white light, the other half of the cycle. With a suitably adjusted flash rate, the luminance of the two components, colored and standard white, is assumed to be equated when, by varying the luminance of the colored component, minimum flicker is perceived. Thus, the perceived magnitude of the flicker is a U-shaped function of the luminance of the variable component, and the minimum of the function defines equal luminance (4). In the study reported here we examined the relation between this psychophysical point of minimum flicker and the amplitude of the evoked brain potential.

We used three observers in all; the data for two of them are presented here. Two alternating stimulus components were presented to the left eye in Maxwellian view as a circular patch, centrally fixated, subtending a visual angle of 3.6 degrees. A concentric white surround, also in Maxwellian view, subtended a visual angle of 31.4 degrees. Thus, the angles subtended by the stimuli approached those considered optimal for flicker photometry (5). The light sources were tungsten-ribbon filament bulbs (General Electric), run at 18 amp. The luminance of the surround field was kept constant and equal to the luminance of the standard white component of the flickering stimulus, namely 368 mlam. Cycling of the flash was controlled by shutters mounted on small stepping motors (6), driven by Tektronix wave-form and pulse generators. Each cycle consisted of a flash of white light followed immediately by a flash of spectral light. Evoked brain potentials were amplified by Tektronix Type 122 amplifiers and were summed with a Mnemotron Computer of Average Transients. The computer was triggered by the output of the same wave-form generator which drives the pulse generators controlling the shutters. Thus, the computer analysis was accurately time-locked with the presentation of the light flashes. A 62.5-msec epoch was used with a sampling rate of 1600 per second. The frequency of stimulation was 16 cy/sec.

Three simultaneous recordings were obtained from the scalp of each observer: (i) bipolar, between the inion and a point 5 cm directly above on the midline; (ii) monopolar, between the inion electrode and a reference