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 waveform 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

electrode behind the right ear; and (iii) monopolar, between the electrode placed 5 cm directly above the inion and the reference electrode behind the right ear. The observer was grounded through an electrode placed behind the left ear. Since the largest and most sensitive response was obtained from recording site iii, only that record is presented here.

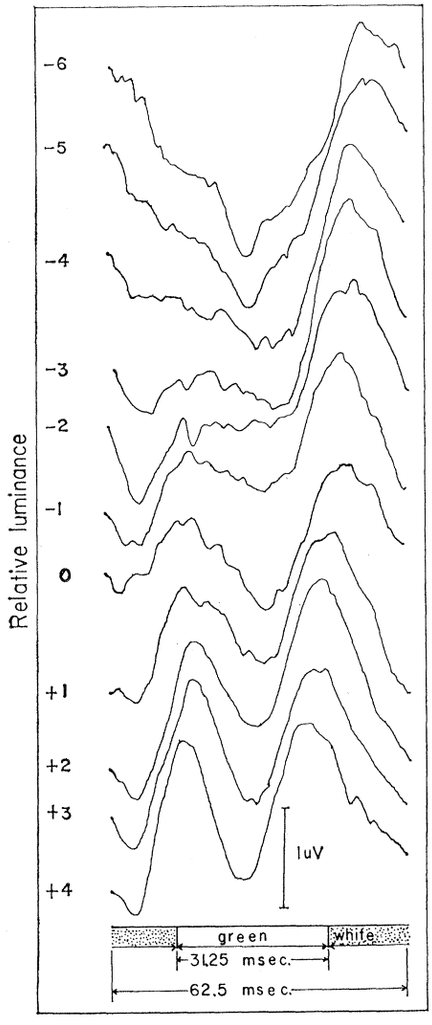

Fig. 1. Tracings of the averaged, monopolar, evoked brain responses for one replication of the green–standard white flicker condition for observer EB. Each curve is the average of 2880 responses. The numbers on the ordinate represent the number of steps of luminance (0.07 log unit per step), relative to the psychophysical match, of the green flicker component. An upward deflection indicates positivity with respect to the visual area scalp electrode. The relation between the stimuli and the responses may be seen at the bottom of the figure. The computer began its sweep in precisely this manner under all conditions. Since the analysis time used was 62.50 msec and the stimulus repetition time was 16 cy/sec analysis "dead" time was negligible for the system used.

Three major stimulus conditions were used: (i) red–standard white flicker, (ii) green–standard white flicker, and (iii) white–standard white flicker. The two color filters used were Baird Atomic interference-type, the red having maximum transmission at 650 nm and falling to 5 percent of maximum at 664 nm and 647 nm, and the green having maximum transmission at 528 nm and falling to 5 percent of maximum at 536 nm and 519 nm.

The observers were dark-adapted for 10 minutes before the beginning of each session. A bite-board was used to assure steady fixation of the flickering field, and an eye patch covered the right eye for the duration of each session. The psychophysical measurements were obtained in the following manner: the luminance of the variable flicker component was changed, by means of a neutral density wedge, in discrete steps of 0.07 log unit, the psychophysical method of limits being used. The observer signaled at each step whether the perceived magnitude of flicker had increased or decreased as a function of the luminance change. Five ascending and five descending series were presented, and the luminance yielding minimum flicker was defined as the mean of the transition points of the ten series.

For the electrophysiological measurements, which immediately followed the psychophysical determination, observers were stimulated over a 3-minute interval, which enabled the on-line summing of 2880 responses. A 3-minute rest interval was allowed between runs, and 13 3-minute averages were obtained in each electrophysiological session. Each of the stimulus conditions was repeated twice, once in an ascending luminance series and once in a descending luminance series.

Figure 1 shows the averaged evoked brain potentials (monopolar) obtained from observer EB for one replication of the green–standard white flicker condition. Figure 2 shows the amplitude of the potentials recorded as a function of the difference in luminance, positive and negative, from the psychophysical point of equality for two observers. The amplitude of response is here defined as the magnitude of the difference in microvolts between the lowest and the highest points of the entire wave-form. Since these curves have been normalized on the abscissa with reference to the point of the psychophysical determination of minimum flicker (0.0), perfect correlation between electrophysiological and psychophysical data would require that all the curves in Fig. 2 have their minimum value at this point. Each function is U-shaped and has a minimum which approaches that of the psychophysical determination. There is a systematic bias in the direction of larger luminance for the comparison light, but the magnitude of the bias in terms of log units of flux is not large. The largest such shift is in the

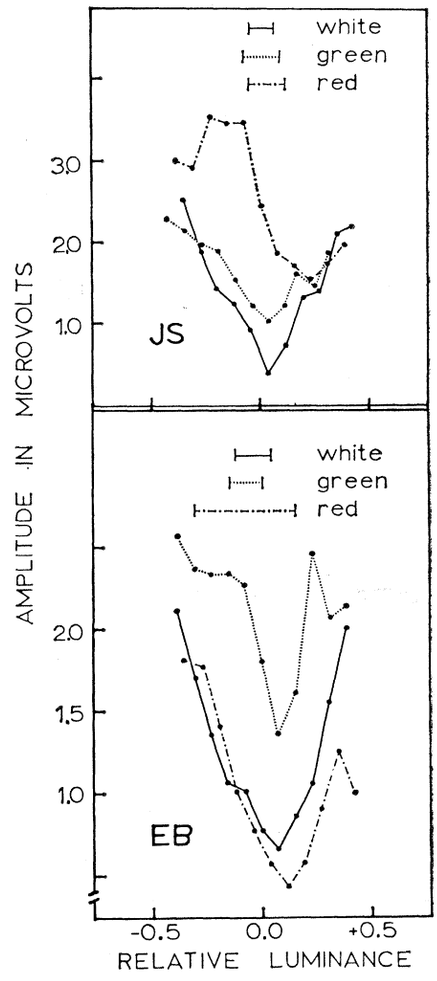

Fig. 2. Amplitude of the averaged evoked brain responses in microvolts as a function of the luminance in log units of the variable flash relative to the psychophysical match for both observers. The results obtained with all three stimulus conditions, averaged over the two replications, are plotted for both observers. The horizontal bars of the legend for each observer indicate both the symbol used for the experimental treatment and the range of psychophysical judgments for that treatment. Note the different ordinate scales for the two observers.

red–standard white flicker condition for observer JS. According to subjective report, this condition produced the most difficult psychophysical judgment as well. The range of the psychophysical judgments is represented by the horizontal bar corresponding to each curve in Fig. 2. The amount and direction of the skewness of psychophysical judgments appears to be well correlated with the bias of the minimum values relative to 0.0 on the abscissa. With the exception of the red–standard white flicker condition for observer JS, the minimum value of each curve in Fig. 2 falls either within, or less than one intensity step (0.07 log unit) outside of the psychophysical range. Examination of these functions also indicates that the ordering on the ordinate of the three curves is different for each observer. The significance of these differences cannot be properly assessed until more data from many wavelength combinations have been collected.

The minimum of the curve for the white–standard white flicker condition in Fig. 2 for observer JS, and that of the curve for red–standard white for observer EB, approach the noise level of the electrophysiological analysis system used. The subjective reports of the observers indicate that there was barely perceptible flicker in the neighborhood of the minimum response. Flicker did not disappear altogether in the white–standard white conditions because of the critical nature of alignment factors under these conditions; however, the alignment was sufficiently good that the magnitude of flicker perceived in this condition was extremely small. The smallest responses obtained were approximately 0.4 μv in amplitude. This indicates that the electrophysiological response can be followed down almost to the perceptual threshold of flicker.

Although the electrophysiological and psychophysical results were compared for conditions in which only white, red, and green stimuli were used, the feasibility of performing flicker photometry by measuring evoked brain potentials is clearly shown (*7*). A comprehensive study covering the entire visible spectrum should also reveal the significance of the individual differences observed and the specific relation between these psychophysical measures and the dimensions of the evoked brain potential. It is quite clear from our study that the evoked brain potential is an extremely sensitive measure of changes in stimulus, and that, when the same rigorous control of stimulus conditions expected in exacting psychophysical experimentation is provided, data of comparable sensitivity are the result.

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Attenuation of Aversive Properties of Peripheral Shock by Hypothalamic Stimulation

Abstract. *Clinical reports of alleviation of pain with positive brain stimulation were investigated experimentally. Rats in a two-compartment testing chamber sought out hypothalamic stimulation and escaped from aversive foot shock delivered through a grid-scrambling device. Animals also sought out paired hypothalamic stimulation and foot shock. Control experiments demonstrating that animals did not discriminate between hypothalamic stimulation and paired hypothalamic stimulation and foot shock supported the view that hypothalamic stimulation attenuates the aversive properties of foot shock.*

There are several reports that brain stimulation modifies aversive states. Heath (*1*), for example, states that patients receiving stimulation of the septal area obtain immediate relief from intractable pain, and Lilly (*2*) comments that positive brain stimulation of monkeys increases the threshold of pain resulting from aversive central stimulation. Until recently there were no quantitative data available on this topic. Valenstein (*3*) reported that animals would seek out aversive stimulation of the dorsomedial tegmentum if it was paired with positive hypothalamic stimulation (*4*). As these tegmental sites receive direct input from the spinothalamic "pain tract" (*5*), it seemed important to determine if hypothalamic stimulation would effectively mask a painful stimulus delivered through peripheral receptors.

Eight albino rats (300 to 400 g) of the Holtzman strain were used. The testing chamber, modified slightly from that described in detail elsewhere (*6*), consisted of a plexiglass chamber (60 by 25 cm and 42.5 cm high) divided into two compartments of equal size. The floor of the chamber was a shock grid constructed of brass rods. Two photoelectric cell assemblies located 3.7 cm above the floor divided each compartment in half. As a rat proceeded halfway into a compartment, the light beam was interrupted and a clock was started. If the rat was in the positive compartment, it received either central or peripheral stimulation or both at a fixed repetition rate. In order to turn off the stimulation or, in later experiments, to change the stimulation conditions, the animal had to break the beam in the compartment opposite the one last entered. A test consisted of either 10 or 20 1-minute periods. The positive compartment was switched on a random sequence which guaranteed that each compartment was positive for half the 1-minute periods during each test. Thus an animal actively seeking out or escaping stimulation could not remain in one compartment. Time in 0.1-second units in the positive and negative compartments was recorded automatically.

Bipolar electrodes, bare only at the cross section, were implanted with the aid of a stereotaxic instrument into the lateral hypothalamus (*7*). The coordinates used were 4.0 mm posterior to bregma, 1.5 mm lateral of the midline, and 8.75 mm below the skull surface. At the completion of the experiment the animals were anesthetized and perfused with saline and formalin. Frozen brain sections, 80 μ thick, were