

that the fly's gaze corresponds to our eye movements (2) as well as to our subjective (and illusory) evaluation of the segment length. Whether flies are actually "susceptible" to the illusion is, of course, a logically separate and still open question.

The effect shown in Fig. 1 can be also expected from the phenomenological theory of the fly's orientation behavior (4, 5). In this theory the way a fly gazes at a pattern consisting of a black vertical stripe turns out to be equivalent to the motion of a particle in a nonharmonic one-dimensional potential well, which is associated with the "attractiveness" profile of the stripe for the fly. The minimum of the potential well gives the most probable direction of gaze (the maximum in the histograms). The potential profile associated with complex patterns composed of more vertical segments can be obtained, as a first approximation (6), by superimposing the individual contributions. Moreover, oblique segments are, in this respect, practically equivalent to their vertical projections (4). From this point of view, Fig. 1a is equivalent to the pairs of vertical bars in Fig. 1b. The potential that can be associated with Fig. 1bII has two minima which are far-

ther apart than those in Fig. 1bI; therefore, the two most probable directions of gaze are expected to be farther apart, in agreement with the experimental results in Fig. 1c.

Therefore, an intriguing possibility is that a similar theory may account for the human eye's movements corresponding to the Muller-Lyer pattern. In fact, the properties required (5) are quite general and are likely to be true for the human fixation system.

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Visually Evoked Magnetic Fields of the Human Brain

Abstract. *Magnetic field variations from the human brain produced by visual stimulation have been observed in a normal laboratory setting with a superconducting quantum interference device and no magnetic shielding of the subject. Previously unknown temporal and spatial features of the field near the scalp are reported.*

Conventional electrical measurements of sensory evoked responses monitor the difference in potential between electrodes applied to the scalp. Since the electrodes are separated from the active regions of the brain by low conductivity tissue and bone, there is only weak electrical coupling between the electrodes and the region in which interesting electrical activity originates. A more direct indicator is the external magnetic field associated with the

flow of strong currents within the relatively highly conductive tissues of the brain, for this field would be little affected by weak currents in the dermis. In addition, the source of the external magnetic field would be more precisely localizable than are the sources of potential change monitored by traditional techniques.

The magnetic field studies of Cohen (1) demonstrated that neural activity of the human brain produces a detectable mag-

netic field outside the head. Cohen observed both spontaneous activity (that is, at alpha frequencies) (2) and visually evoked responses (3, 4). The field is exceedingly weak, and Cohen's success depended upon the use of elaborate magnetic shielding to reduce the ambient field of terrestrial origin to a level below that of the brain's field. Our results demonstrate that it is possible to measure the evoked magnetic field of the brain without shielding and with relatively modest additions to the normal complement of equipment needed to measure potentials, thus making the phenomenon of neuromagnetism suitable for study in many laboratories. Our initial results also reveal some previously unknown characteristics of the magnetic response to a visual stimulus.

Temporal variations of the magnetic field near the scalp associated with brain activity have a peak-to-peak value of about 2×10^{-8} gauss for spontaneous activity at alpha frequencies, and about 5×10^{-9} gauss for visually evoked responses. The advent of the superconducting quantum interference device (SQUID) (5) provides a field monitor of sufficient sensitivity to detect such fields. The SQUID is maintained at liquid helium temperature in a Dewar made of glass and fiberglass (6), and is coupled to external fields by a loop of superconducting wire (a "flux transformer") mounted in the tail section of the Dewar, as illustrated in Fig. 1. The flux transformer is wound in the configuration of a second-order gradiometer (7); three coaxial coils 2.2 cm in diameter, separated by equal distances of 3.9 cm, each end coil with one turn of wire wound in the same sense, and the center coil with two turns wound in the opposite sense. This configuration is used to discriminate against the major sources of noise, changes in the ambient field due to micropulsations caused by disturbances in the upper atmosphere and other local sources which produce relatively uniform fields. In our laboratory the amplitude of this ambient noise is about 10^{-2} gauss. The second-order gradiometer is found to be less sensitive to vibration-induced noise than a simpler two-coil gradiometer.

To balance the flux transformer for minimal response to uniform fields, three orthogonal pairs of trim coils are wound in series with the second-order gradiometer. The effective area of the trim coil is then adjusted with superconducting shields to achieve minimal noise. After balancing, our peak-to-peak noise is typically 3×10^{-8} gauss for a bandwidth of 5 to 25 hz. There is substantially more noise below 5 hz from the low frequency content of the ambient field. The inherent noise from the SQUID and flux transformer of 8×10^{-10}

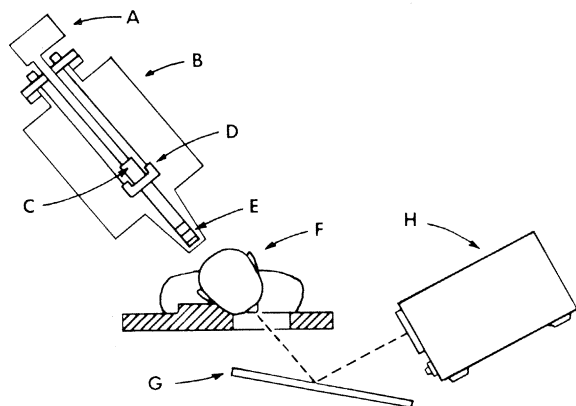


Fig. 1. Arrangement for monitoring evoked response: (A) SQUID electronics; (B) Dewar; (C) SQUID; (D) trim coils; (E) second-order gradiometer, the end coil of which is the pickup coil; (F) subject prone on table; (G) mirror; and (H) oscilloscope for presenting stimulus.

gauss $\text{hz}^{-1/2}$ is not a limiting factor in the present experiments. The Dewar in our laboratory is located about 1.5 m above a steel-reinforced concrete floor on the ninth story of a building in Manhattan. The laboratory is about 40 m directly above a subway, and occasionally the effects of a passing train can be detected.

The visual stimulus in our experiment was a retinally vertical bar grating of moderate luminance on an oscilloscope screen, flashed on for 50 msec and off for 50 msec to produce a 10-hz flicker. There were 6.5 bars on the 10-cm-wide screen, which was located about 120 cm from the subject's eyes. The subject was instructed to maintain fixation on a small black spot mounted in the center of the screen throughout each 2-minute trial. For some measurements the subject looked at the virtual image of the display in a mirror. The output of the function generator which caused the bar pattern to be turned on was also applied as a trigger to an averaging computer (PAR waveform eductor), to permit the detection of average evoked responses in real time. The same trigger and observed signal were recorded on an Ampex FM instrumentation recorder for subsequent processing on a PDP-12 computer.

Average responses were measured without the subject in place, to check for the existence of artifacts. None were found. Three subjects have been studied, and their responses were essentially the same, differing only in amplitude and precise location on the scalp. Because of space limitations we report only results obtained with the most extensively studied of the three subjects.

The data from our subject for the component of the field normal to the scalp are shown in Fig. 2. The sets of curves A and B in the figure are tracings of plots generated to scale by the PDP-12 computer, which averaged 1000 sweeps. The tracings in column A are responses obtained when, from a distance of 2 cm from the scalp, the end pickup coil of the second-order gradiometer was centered over different positions on the midline of the scalp above the inion. The lowest tracing was obtained from a position 3.2 cm above the inion, and the power of this signal is not significantly greater than that of the average noise power. Noise measurements were obtained with the observer's eyes closed and also with them open but with the averaging computer triggered at a frequency slightly different from the frequency of the stimulus. Such a technique made it possible for us to measure noise with the level of spontaneous brain activity identical to that which is present when the observer is actively looking at a stimulus. In addition,

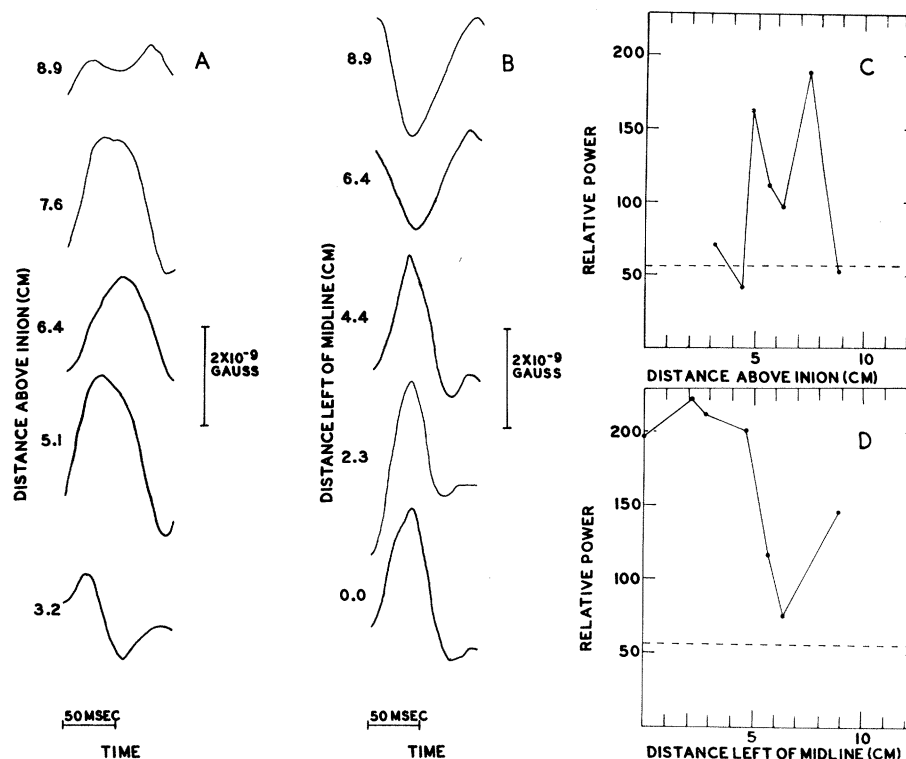


Fig. 2. Response (A) and response power (C) as a function of distance above the inion on the midline; response (B) and response power (D) as a function of distance to the left of the midline, 7.6 cm above the inion. Curves A and B are an average of 1000 sweeps. An upward deflection indicates that the field is directed away from the scalp. In (C) and (D) the dashed lines represent the average noise power for all trials.

noise measurements were made with the oscilloscope screen covered, and with the subject absent. All of these control conditions reveal no artificial responses.

As indicated by the curves in Fig. 2A, a significantly large and repeatable response occurred 5 cm above the inion and at higher points up to about 8 cm above the inion. At still higher points the responses became unreliable and were commensurate in power with the noise level. As borne out by the summary in Fig. 2C, strong responses could be detected only in a 3-cm-long region on the midline of the scalp (8). This localizability may be contrasted with the classic evoked potential, which is widespread and can be detected on most of the scalp (9). The magnetic response is clearly localized in the vicinity of the visual areas of the brain.

The curves in Fig. 2B represent responses with the pickup coil centered 7.6 cm above the inion and at positions to the left of that point. It can be seen that as the position of the probe is shifted toward the left side of the head, the response remains nearly constant until we reach a point more than 5 cm to the side of the midline. Beyond this point the response reverses in phase. This reversal takes place between 5 and 6.4 cm to the side of the midline. These features indicate that the response 50 msec after initiation of the stimulus produces a field near the midline that

is directed outward from the back of the scalp and that the field turns inward at the side. The response at 0 cm in Fig. 2, B and D, was obtained from the same position as the response at 7.6 cm in Fig. 2, A and C, but after the subject had a 1-hour rest period and was repositioned in the apparatus. The close agreement of results indicates the good reproducibility which we generally have obtained. Similar response patterns were observed from two other subjects. More complete mapping of variations in response with position of the probe is now under way. We are also studying the effects of varying the orientation and spatial frequency of the display, and moving the stimulus.

We have achieved some success in recording responses at lower stimulus frequencies, as detected by Cohen (3) and Reite *et al.* (4). Our noise level increases substantially below 5 hz, but we believe it is possible to improve the balance of the flux transformer by a factor of 2 or 4, thereby increasing the possibilities for studying these more textured responses without shielding.

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8. "Relative power" on the axes of Fig. 2, C and D, refers to the mean square observed field. The ratio of the mean square field of the response to the mean square field obtained on noise trials is equivalent to the F ratio of classical statistics. For these figures, 500 sweeps at twice the stimulus period, used in signal averaging, correspond to 500 degrees of freedom; therefore $F > 1.2$ has a probability $P < .01$ of occurring if only noise is present. Responses with a power greater than 65 are considered highly significant.
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10. This work was supported by the National Science Foundation, the National Institutes of Health Biomedical Sciences support grant to New York University, and the New York University Arts and Science Research Fund. We thank D. Cohen and W. S. Goree for their useful comments and suggestions.

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Multidimensional Variation in an Avian Display: Implications for Social Communication

Abstract. *An analysis of song-spread displays performed in social communication by carib grackles, Quiscalus lugubris, revealed that two components of this motor coordination, beak elevation and wing elevation, varied independently. Variation in each depended strongly on the performer's social context, an indication that these components simultaneously reflected different behavioral tendencies of the performer. Independent variation in the elements of a display can permit transmission of more information per display about the performer's behavioral state.*

Male and female carib grackles, *Quiscalus lugubris*, perform a complex coordination, the song-spread display, both when courting the opposite sex and when near rivals of the performer's own sex. Early ethologists recognized the importance of such discrete classes of actions in the social behavior of many animals. These action patterns sometimes attain surprising degrees of stereotypy in repeated performances by one individual or within a population, although most vary substantially in both respects (1-3). Because many of these discrete action patterns serve primarily for communication with social partners, the variation or stereotypy in displays requires examination in the framework of the species' requirements for social communication.

The information available to social partners will depend in part on the variability of an action pattern and on the covariation of its elements with the performer's behavioral tendencies, as indicated by the social circumstances or by preceding and following actions (4). This report, a multivariate analysis of a communicatory display, documents for the first time an action pattern with independently varying components, each associated with different social contexts. This evidence suggests that patterns of variation in this display increase the information available about the performer's behavioral state.

The carib grackle's song-spread display, probably homologous with similar displays

of related species, such as the familiar common grackle, *Q. quiscula* (5), involves synchronized movements of all of the animal's extremities. It comprises at least eight motor elements (Fig. 1): (i) a vocalization, (ii) dorsad rotation of the cranium so that the beak is lifted, (iii) elevation and slight extension of the wings, (iv) rapid fluttering of the wings in periodic bouts, (v) dorsad rotation of the deeply keeled tail so that the outer edges of the tail slightly pass vertical, (vi) alternating extension and flexion of the legs to impart a bouncing motion to the body, (vii) irregular movements of the gray nictitating membrane across the yellow iris, and (viii) partial erection of the ventral and anterior contour plumage. The last seven components all vary considerably from performance to performance by the same individual, to the extent that

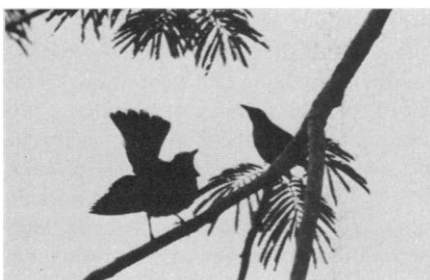


Fig. 1. Male carib grackle performs a song-spread display (left) while facing another male in a weak version of the bill-up display (right). Photographed at Fundo Pecuario Masagualar, Guárico, Venezuela.

this variation greatly exceeds any consistent differences between individuals. The observations reported here pertain to performances by a number of individuals in one nesting colony. The position of the tail during the display varied considerably less than did the orientation of the beak and the movements of the wings. Consequently, the following discussion primarily deals with variation in the elevation of the beak and wings. Females performed song spreads much less frequently than did males.

For these studies I observed male and female grackles from distances of 5 to 10 m while they displayed on the low branches of an isolated tree used by the grackles for nesting. The study was conducted 3 km west of Arima, Trinidad, West Indies, in July 1971. For every song spread observed in clear view during hour-long watches, I systematically dictated the performer's sex, the maximum wing elevation (in intervals of 15° above the resting position), the maximum beak elevation (in intervals of 10° with respect to horizontal), the performer's social context (whether a male, a female, or no other bird was less than 1 m away), and temporal context (whether or not the bird performed bill-up displays, indicative of aggressive tendencies, immediately before or after the song spread). I was close enough to the displaying grackles to see the movements of the beak and wings clearly. In any one minute, I recorded data only once from the same individual.

These observations allowed me to determine the frequencies with which each sex performed song-spread displays with different combinations of beak elevation, wing elevation, social context, and temporal context. Because the extremes of either beak or wing elevation occurred relatively infrequently, for the following analyses I condensed each of these parameters into two classes, higher and lower elevations, divided as near the median as possible (6). The complete data for song-spread displays by each sex thus constituted a contingency table in four dimensions: beak and wing elevation (each with two categories), social context (with three categories), and temporal context (with two categories).

To test for associations among beak elevation, wing elevation, and social context in males' displays, I required a non-parametric analysis of independence for the corresponding three-dimensional (2 by 2 by 3) matrix, for which the G statistic provides an appropriate procedure (7). A three-way analysis with the G statistic established, with negligible chance of error, that these three variables lacked joint independence (Table 1). The levels of both beak and wing elevation depend strongly