

more such animals in a sample of six is only about 3 percent. Animals with low error scores like those of animals Nos. 8 and 9 are at least as rare, and the probability of two such animals in a sample of six is therefore at least as low. To find four such deviant animals in a sample of six is even less likely.

The best evidence that our grafting procedure affected both the brains and the behavior of our experimental animals may be found in the correlation between the brain structure and the behavior. The two animals with normal brains (Nos. 1 and 6) behaved normally. The probability of this correspondence alone is only about 2 percent. Furthermore, the two animals with unusually low error scores (Nos. 8 and 9) showed tectal thickening which was restricted to the caudal region, whereas the two animals with progressive improvement (Nos. 4 and 10) showed changes in the anterior tectum (No. 10 a new structure; and No. 1, a general thickening that included the anterior region). Our results thus suggest that supplementation experiments have an important role to play in the analysis of brain function.

DAVID E. BRESLER

Department of Psychology,
University of California,
Los Angeles 90024

M. E. BITTERMAN

Department of Psychology,
Bryn Mawr College,
Bryn Mawr, Pennsylvania 19010

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3. J. M. Oppenheimer reports (personal communication) that animals were quite unlikely to survive after the depletion of their yolk sacs because the operation usually produced peripheral anomalies, such as faulty mouthparts, which might have led to death from starvation.
4. That the behavioral technique used here for *Tilapia* is appropriate also to *Fundulus* was demonstrated about 10 years ago. The behavior of *Fundulus* was examined out of interest in the possibility of just such experiments as are reported here. See N. Longo and M. E. Bitterman, *Amer. J. Psychol.* **72**, 616 (1959).
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They were directed medially approximately 4 mm inward from the lateral surface and about 1 mm below the dorsal surface of the superior temporal gyrus. Nine electrodes were implanted similarly, but on one side only, in the auditory cortex of a second monkey (M-10). The surgical procedure and method of implanting electrodes have been described (2). Intracranial stimulation through pairs of electrodes was provided by an isolated constant current generator, with a continuously variable 60-hz output of from 1 to 1000 μ amp (root mean square).

Bipolar and monopolar evoked potentials elicited by pure tones were recorded from these electrodes. For monopolar recording the indifferent electrode consisted of five screws distributed around the skull. Potentials were recorded with standard neurophysiological equipment, including Grass P511 preamplifiers and a Tektronix oscilloscope. Frequency response of the system was limited by low and high half-amplitude filters set at 3 hz and 2 khz. Signals from the preamplifiers were also fed to the analog-to-digital converter of a Digital Equipment Corporation (PDP-8) computer for on-line analysis. The computer was programmed, first to sample (at 4 khz) a 100-msec episode of cortical activity starting from the onset of the tone, and then to determine the latencies of the first positive-going peak and the first negative-going peak, and the peak-to-peak amplitude of the signal (3). This procedure was followed for each evoked potential. Statistics based upon these individual measurements were then calculated.

The behavioral procedures have been described (2, 4). Training and testing were conducted in a sound-deadened, electrically shielded, double-walled experimental chamber (Industrial Acoustics). During experimental sessions each subject was restrained in a standard primate chair. Each subject's head was further restrained so that Permoflux (PDR-600) earphones could be placed directly over the external auditory meatus. The sound generation and calibration equipment and procedures have been described (5). The tone was electrically switched with a rise and fall time of 5 msec. Intensities of all tones were measured at the opening of the external auditory meatus with a calibrated probe tube and Bruel and Kjaer condenser microphones. All sound intensities given in this report are in decibels relative to 0.0002 dyne/cm².

Evoked Potentials and Auditory Reaction Time in Monkeys

Abstract. Monkeys with bipolar stimulating and recording electrodes in primary auditory cortex were trained to release a key to the onset of a pure tone. Substitution of direct cortical stimulation for the pure tone resulted in a reduction of 15 milliseconds in the latency of the behavioral response. This changed latency agreed with the latency of the primary evoked potential recorded from the animals. Systematic related changes in the amplitude of the central response and in the latency of the behavioral response followed changes in the intensity and frequency of the acoustic stimulus.

Monkeys can be trained to respond rapidly (within 200 msec) to the onset of acoustic stimulation. Replacing the acoustic stimulus with direct electrical stimulation through electrodes in the primary auditory cortex results in a more rapidly executed behavioral response. This shift in latency agrees with the initial latency of the acoustically evoked primary potential recorded from the same electrodes. Moreover, concurrent behavioral and electrophysiological measurements indicate that

characteristics of the evoked potential and behavioral response vary systematically with changes in the frequency and intensity of the acoustic stimulation. The findings suggest an effective approach to the study of relations between cortical function and behavior.

Bipolar platinum-iridium electrodes were implanted bilaterally in the primary auditory cortex (I) of a monkey (M-9) (*Macaca irus*). The electrodes were placed when sufficient bone was removed to reveal the fissural patterns.

The monkeys were trained to press a telegraph key at the onset of a light, to hold the key down during a variable period (1 to 4 seconds), and to release the key upon presentation of a pure tone. Later, direct electrical stimulation of the auditory cortex was substituted for the pure tone. Release of the key in the presence of the light and tone was followed by a delivery of a 190-mg banana pellet (Ciba). To obtain minimum reaction times (RT's) to tonal stimulation, delivery of the banana pellet was made contingent upon responses with short latency during training (6).

Solid-state circuitry included in and peripheral to the PDP-8 computer was used to program the conditioning procedures and to monitor behavioral performance. This means of control permitted automatic variation of the parameters of the peripheral stimulus during each experimental session. The latency of key release following tone onset, as well as the statistics calculated from the evoked potential, were punched on paper tape by the computer for off-line analysis.

After the animals were trained, the latencies of behavioral responses for monkeys were comparable to human RT's. Minimum behavioral latencies for these monkeys ranged from 175 to 200 msec. Similar to observations on the visual system, behavioral responses were easily transferred from acoustic to direct electrical stimulation of the auditory cortex (2).

Figure 1 (left) illustrates the effect of variation in intensity of a pure tone and of direct electrical stimulation of the auditory cortex on behavioral latencies in monkey M-9. For both stimuli RT's vary in the same manner. With increasing intensity both median RT and RT variability decreased asymptotically. At intensities yielding the brief latency responses, a consistent 15-msec difference occurred between RT's to acoustic and cortical stimulation. Observations of the evoked potential recorded differentially between the two electrodes used to stimulate the cortex in this monkey are illustrated in Fig. 1 (right). At each intensity five traces of the evoked potential have been superimposed. Characteristics of this potential, primarily the initial latency, suggest that it is similar to the "primary" evoked potential observed in anesthetized animals. Initial latency of this primary evoked response to high-intensity tones is approximately 15 msec. With changes in the intensity of

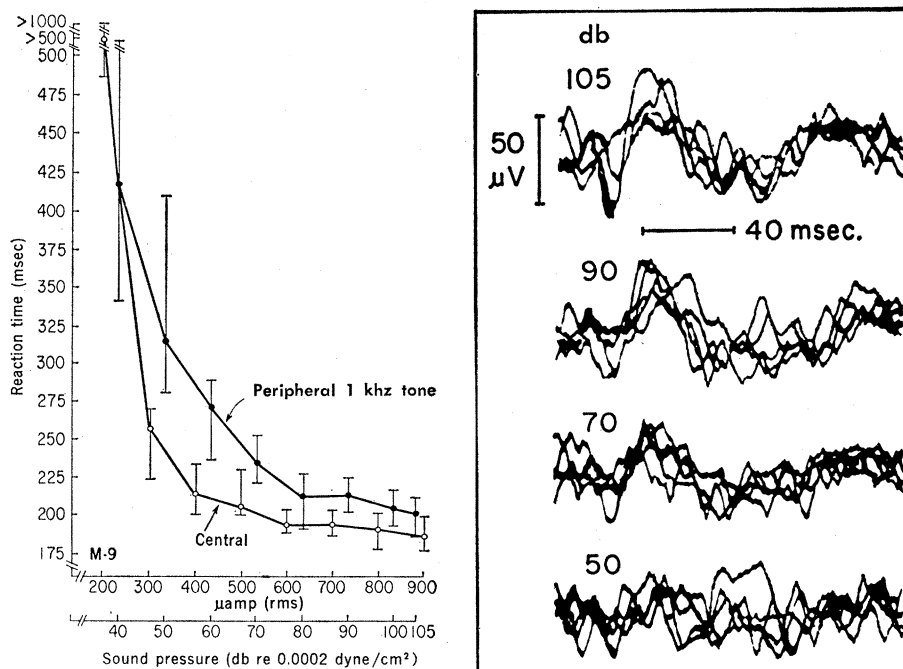


Fig. 1. (Left) Median RT's (ordinate) as a function of 1-kHz tone at various intensities and as a function of direct stimulation at various intensities (abscissa). Vertical bars are interquartile ranges. (Right) Differentially recorded evoked potentials from behaving monkey (M-9) to 1-kHz tone. Recordings were made between the same two electrodes used to stimulate this cortex. Each response set is comprised of five superimposed single responses. Fast vertical deflections were retouched to prevent loss in photography.

the tone, over a range in which the evoked potential could be reliably measured with our techniques, little consistent change in the initial latency of the evoked cortical response was observed. However, amplitude of the evoked response appeared to be directly related to stimulus intensity.

The covariation in amplitude of the

evoked cortical potential and latency of the behavioral response to changes in the intensity of the stimulus is illustrated in Fig. 2. These data were obtained from M-10 over several sessions. Plotted RT's represent medians for at least 50 trials at each intensity. The measurement of amplitude of the evoked response is based upon computer-calculated me-

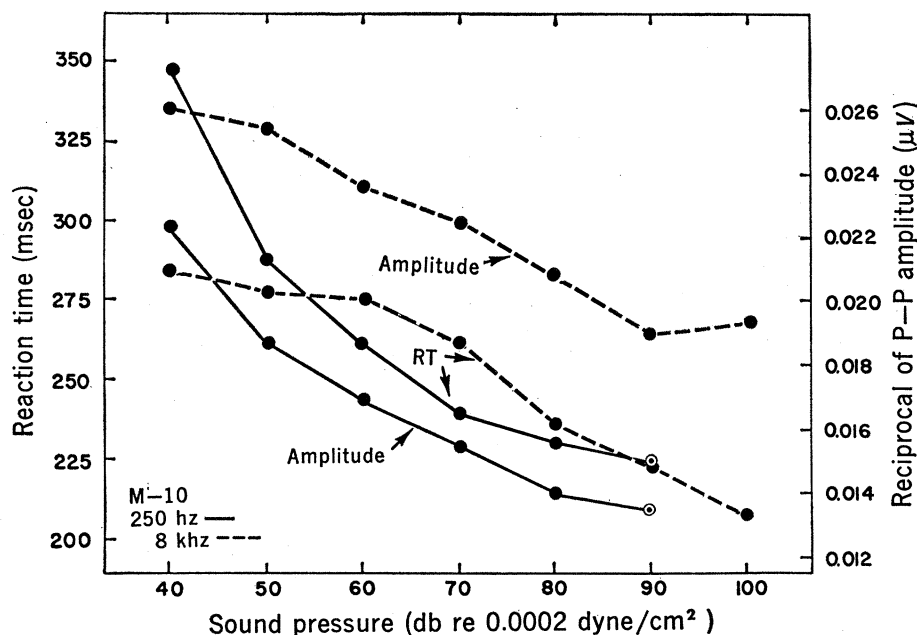


Fig. 2. Median reaction times and reciprocals of the peak-to-peak amplitude of evoked potentials recorded simultaneously from monkey M-10. Measurements were taken to 250-hz and 8-kHz pure tones at various sound-pressure levels.

dian amplitudes derived during these same behavioral trials. Reciprocals of the peak-to-peak amplitude have been plotted. The similarity in variation of the evoked potential amplitude and RT observed at 250 hz represents one of the clearer observations of this relationship. Curves at 8 khz represent average observations. For the 8-khz curves, both RT and the reciprocal of evoked potential amplitude increased rapidly at the next lower intensity (30 db). However, the amplitude of the evoked potential was reduced to a point where peak-to-peak amplitude could not be reliably measured with our procedure.

It has been suggested that the evoked potentials recorded in this investigation are "primary" evoked potentials. If this is indeed the case, and if the response reflects neural activity involved in elicitation of the behavioral response, one questions the lack of obvious changes in the latency of the cortical response with changes in the intensity of the stimulus. A possible explanation that may account for this is: observations on primary evoked responses have shown that most rapid latency changes occur at and near threshold levels of stimulation. At higher intensities latency changes are minimum. It may be that the intensities used in this investigation were at a level producing only minimum changes in latency. Latency dispersion as the activity continues through the synaptic system involved in this behavior would account for the latency changes observed in the reaction times.

Similar procedures have been used to demonstrate that when direct visual cortex stimulation was substituted for photic stimulation, behavioral response latency shifted by 30 to 39 msec. This behavioral response shift may be compared to the 15-msec response shift observed in the auditory system. Both latency shifts agree approximately with the latency of the peripherally evoked primary potential recorded differentially through the stimulating electrodes. This observation, plus the ease with which behavioral responses transfer from peripheral to central stimulation, suggest that in the monkey the cortex may function in the control of this behavioral response.

One of the primary advantages of the procedures we used is that they yield evoked potentials of sufficient stability to permit individual analysis and study, without the necessity of summing devices in unanesthetized

animals. The potential appears to be the primary evoked potential; thus an extensive literature on its properties and the possible basis for its generation is available from neurophysiological investigations. These advantages apply to the stable and extensively studied reaction time response. The characteristic stability of these measures suggests that they are suitable for individual trial comparison. Furthermore, the relation between the temporal characteristics of the behavioral response and the temporal and amplitude characteristics of the neurophysiological event provides a meaningful basis for comparison and subsequent study of the relation of cortical function to behavior.

JOSEF M. MILLER*

DAVID B. MOODY, WILLIAM C. STEBBINS
Kresge Hearing Research Institute,
University of Michigan Medical Center,
Ann Arbor 48104

Avena magna: New Oat Species

An annual species of oats, described (1) as *Avena magna* Murphy and Terrell (sp. nova), is a tetraploid, $2n = 28$. It is related to the well-known hexaploid *A. sterilis* of the Mediterranean shores with a center of origin and dispersal in Asia Minor. The new species was found, by Zillinsky, near Rabat in Morocco, within the area of *A. sterilis*.

This is a very important discovery, since among the annual species of oats (*Avena* sect. *Avena*) there have long been known several species of a polyploid series: *A. strigosa*, $2n = 14$; *A. barbata*, $2n = 28$; and *A. fatua* and *A. sativa*, $2n = 42$.

In 1953 I found a strange form of oats near Sassari in Sardinia. At first I did not hesitate to refer it to *A. sterilis*, because it differed only slightly from this species, in a weaker habit and fewer and more sturdy spikes. These features did not justify referral to another form. However, I found it to have $2n = 28$ chromosomes, instead of $2n = 42$ typical of *A. sterilis*. Therefore, I pointed out (2) that a tetraploid biotype of *A. sterilis* occurs in Sardinia. The karyogram of this taxon was carefully analyzed. The chromosomes range in size from 5.9 to 2.6 microns, and the karyotype was found to include one pair with satellites, six pairs with a median centromere, and seven pairs with a submedian or subterminal centromere.

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* Present address: Departments of Physiology-Biophysics and Otolaryngology, University of Washington School of Medicine, Seattle 98105.

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According to Murphy *et al.*, the karyotype of the new species shows two pairs with satellites, four pairs with a median centromere, and eight pairs with a submedian or subterminal centromere. The differences from my observations are small and caused by difficulties of observation, since the second pair of satellites is very small and I was in doubt as to inclusion of two pairs in the median or submedian category. I have no doubt that the plant studied in Sardinia is identical to that described by Murphy *et al.* from Morocco, both morphologically and karyologically.

I left Sardinia in 1956, and later botanists have not found the tetraploid there, probably because it is easily confused with the hexaploid *A. sterilis*.

Murphy *et al.* apparently were unaware of my publication, though the chromosome number was listed (3) in 1959. The apparently wider distribution of the tetraploid may be of some interest to cytotaxonomists.

GUISEPPI MARTINOLI

Botanical Institute, University of
Pisa, Pisa, Italy

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