The substitution of $\int S$ for the linear shortening term (S) as a parameter of energy utilization is not as self-evident as the introduction of the $\int P$. The main difference between the two curves is a greater degree of curvature in the case of $\int S$. If shortening (S) is used in Fig. 5 instead of $\int S$, the small trough at 7*g* is eliminated in the top curve, and a continuously convex relation results.

Our evidence is in agreement with the notion that muscle contraction can be regarded as a series of sequential chemical reactions (*14*). Force arises and is maintained as one step in this sequence. Shortening may constitute another such step occurring either in series or in parallel to the reaction producing the force. In the case of an isometric contraction, in which shortening is practically zero and the internal work is no more than 10 percent of the total energy utilization, force production is virtually the sole energy-consuming activity. Thus, tension may be looked upon as the index to the intensity and the time-course of one step in the sequence of reactions initiated by the action potential. For unbranching systems of sequential, chemical reactions it can be shown that the time-integral of the increase and decrease in concentration of one of the intermediates is linearly related to the total amount of the final product resulting from the overall reaction (*14*). In the case of muscular contraction, it is proposed that shortening and production of force can be treated as mechanical manifestations of the time-course of the concentration of two sequential intermediates or two reaction pathways originating from a common intermediate.

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19. Supported by grants from the Muscular Dystrophy Association of America, Inc.

7 September 1966

Oxygen Tension Changes Evoked in the Brain by Visual Stimulation

Abstract. *Localized changes in oxygen tension were recorded with platinum cathodes placed in the lateral geniculate nucleus in both anesthetized and awake cats. The amplitude of the responses increased with increasing stimulus intensity, but decreased with increasing flash rate. Both increases and decreases in cathode current were produced by steady illumination. The characteristics of the responses suggest that the responses reflect localized variations in blood flow, produced in turn by changes evoked in the tonic neural activity of the lateral geniculate nucleus.*

Localized temperature changes can be evoked in the cat's brain by natural stimulation (*1, 2*). Light flashes evoke thermal changes in the lateral geniculate nucleus but not in the inferior colliculus, while auditory stimuli evoke thermal changes in the colliculus but not in the geniculate nucleus (*1*). Somatic stimulation evokes temperature changes localized in the ventrobasal nucleus in the thalamus (*2*). Elevations in the temperature of the entire brain during paradoxical sleep and arousal have also been reported (*3*). Such temperature changes may result from variations in cerebral blood flow and metabolic heat output, and they are probably accompanied by variations in the oxygen tension of the tissue. The oxygen tension of tissue can be indirectly assessed with bare oxygen cathodes consisting of platinum wire negatively biased with respect to a nonpolarizable reference electrode. Such cathodes have been used to determine variations in the concentration of oxygen in brain tissue during hypoxia and hyperoxia, stimulation of the hypothalamus, and during avoidance conditioning in unrestrained cats (*4*). We here report changes in oxygen tension in the lateral geniculate nucleus (LGN) of cats. The changes were evoked by visual stimulation and were recorded by platinum oxygen cathodes.

Twenty-one cats were anesthetized with moderate doses (30 mg per kilogram of body weight) of sodium pentobarbital injected intraperitoneally; supplementary doses were given when necessary during the experiments. The cats were held in a stereotaxic instrument, and the cathodes were inserted through a hole, 1 cm in diameter, trephined through the skull. Recordings were also taken from two unanesthetized cats with cathodes permanently implanted in the LGN. The unanesthetized cats were allowed 1 week to recover from surgery before they were tested. Their line of vision was directed toward the stimulus source by means of a restraining box. In all animals, the pupils were dilated with Cyclogyl during testing, and the cathode placements were verified by standard histological techniques.

The oxygen cathodes were made of platinum–iridium wire (10 percent Ir), 0.5 mm in diameter, and insulated, except at the tip, with Insul-X. The reference electrodes usually consisted of large-area silver electrodes inserted under the temporal muscles, and the cathode bias ranged from 0.5 to 0.8 volt. The current through the electrodes was measured with Grass (7P1A) d-c amplifiers. Light flashes were produced by a Grass photostimulator (PS2D), with flash rates in the range of 2 to 50 per second, flash duration of 10 μsec, and estimated intensities at the cat's eyes of about 2.5×10^5 lux and 2×10^6 lux. Background intensity was about 200 lux.

Consistent increases in the cathode current were evoked in the LGN by flashing light in 11 of the anesthetized cats and in both unanesthetized animals. The responses were approximately 5 percent above the base current, with latencies of 5 to 10 seconds (Fig. 1). The cathode current increases were usually maintained throughout the pe-

riod of stimulation. The amplitude of the responses increased with increasing stimulus intensity, but decreased with increasing flash rate(Fig. 1, C–F). Steady light elicited an increase in cathode current in one cat and consistent decreases in another (Fig. 1, G and H). Responses were not observed in five cats in whom the cathodes were outside the LGN. When recordings were taken simultaneously with cathodes placed in the LGN and midbrain, cathode current changes were recorded from both areas during systemic vascular changes induced by pinching the paw, while changes localized only to the LGN were observed during visual stimulation. In three of the anesthetized cats, oxygen cathode responses could not be evoked by visual stimulation although the cathodes were definitely in the LGN and evoked electrical potentials were recorded. These negative recording sites overlapped with sites that provided cathode responses in other animals. Also, cathode current changes in the inferior colliculus and thalamic ventrobasal nuclei have not been observed, although thermal responses evoked by clicks or somatic stimulation have been recorded in these areas (*1, 2*).

Rhythmic activity was also recorded by the cathodes from the lateral geniculate nucleus and inferior colliculus. The frequencies were in two ranges: 3 to 12 per minute and about 1 per minute (Fig. 1, part I). In lightly anesthetized or conscious animals, these rhythms appeared to be unrelated to breathing, heart rate, or any similar function.

The long latencies of the evoked responses suggest that the oxygen cathode changes are vascular in origin. They may be produced by an increase in the concentration of oxygen in the tissue or by the relative displacement of blood vessels towards the cathode tip during vasodilation. The variation in the amplitude of the responses as a function of intensity and frequency of stimulation corresponds to the variation in tonic neural firing reported by Arduini and Pinneo (*5*); this variation indicates that the vascular activity in neural tissue is partially controlled by the general extent of neural firing of the tissue. Similarly the systemic changes in cerebral blood flow that occur during arousal (*6*) suggest that tonic changes in neural firing also occur during conditions of arousal. It should be possible to observe variations in the concentrations of oxygen in all areas of the brain where large changes in neural firing can be induced by sensory stimulation. The failure to evoke such responses in the inferior colliculus and thalamic ventrobasal nuclei has yet to be explained.

Rhythmic slow potentials (*7*) have been recorded from the brain with frequencies within the range of the oxygen rhythms reported here. Moreover, studies of brain temperature in unanesthetized animals during behavioral tests (*3*) reveal variations that are similar to the slow potential changes that can be recorded from the brain under comparable conditions of arousal (*3, 8*). These temperature changes reflect variations in cerebral metabolic heat and vascular activity (*1, 2*). Since a close correlation between tonic neural activity and vascular activity has been indicated by this study and also by McElligott and Melzack (*1*), it would seem that all of these relatively slow variations in brain potential, temperature, and oxygen tension reflect changes in the electrical activity of large populations of neurons.

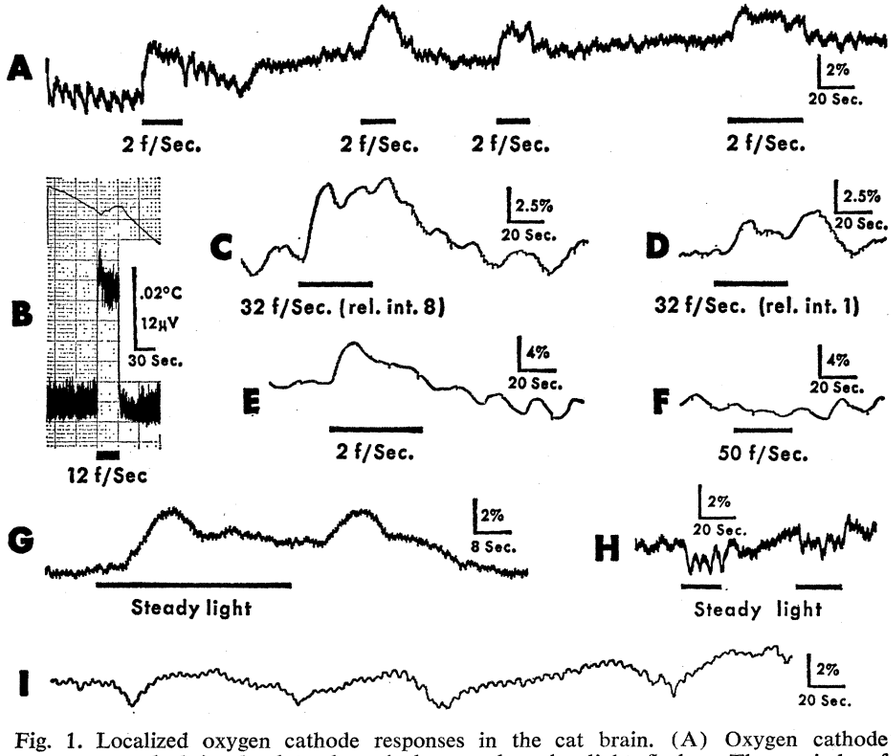

Fig. 1. Localized oxygen cathode responses in the cat brain. (A) Oxygen cathode responses evoked in the lateral geniculate nucleus by light flashes. The periods of stimulation are indicated by the bars. (B) Multiple-unit electrical (bottom) and thermal (top) responses evoked in the lateral geniculate nucleus by flashing light. The electrical record was obtained with a Ballantine root-mean-square voltmeter. The thermal record is 6 seconds in advance of the electrical record. (C, D) Variation in the amplitude of the oxygen cathode responses as a function of the intensity of stimulation. The stimulus intensities were 2×10^6 lux (relative intensity 8), and 2.5×10^5 lux (relative intensity 1). (E, F) Variation in the amplitude of the oxygen cathode responses as a function of rates of stimulation. (G) Increase in the oxygen cathode current in response to steady illumination. (H) Decreases in oxygen cathode current in response to steady illumination. (I) Slow rhythmic activity (0.8 per minute) recorded from the brain by the oxygen cathode. The breathing rate was 12 per minute.

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9. Supported by contract SD-193 from ARPA. We thank J. G. McElligott for assistance in carrying out these experiments and for providing the record shown in Fig. 1B. This paper is based on a thesis submitted by K.J.G. for the M.S. degree at McGill University.

2 March 1967