

later glacial stage than the Illinoian that this concentrate was formed in a very short time, largely by wind action. As matters now stand, there seems need to determine whether or not this concentrate was formed in a short time. The mere declaration that it was formed rapidly is not to be taken as decisive, even if several geologists unite in the declaration.

The present writer is also skeptical of an interpretation which restricts the glaciation of one stage to the eastern part of the continent and of a succeeding stage to the central part of the continent, for in the Nebraskan, Kansan and Wisconsin stages there was glaciation over both the eastern and the central part. It thus seems more natural for the Illinoian of the eastern part to have its equivalent in the Iowan of the central part.

In the above estimates it was calculated that if the third or Illinoian glaciation covered only the eastern part of the continent it may have lasted only about 50,000 years, or from 210,000 down to 160,000 years ago. But if it covered the central as well as eastern part of the continent and embraced the Iowan it is likely to have lasted 75,000 years, or down to 135,000 years ago.

Summing up the matter of the relative proportion of time involved in the Pleistocene glacial and interglacial stages, it appears that fully 75 per cent. of the last 200,000 years has been under glacial conditions, but that prior to this the interglacial conditions were prevalent for at least 75 per cent. of the time. If then the entire Pleistocene period embraces a million years, the glacial conditions were prevalent for about 300,000 years, and the interglacial conditions for about 700,000 years, of which some 50,000 years, falling in the Sangamon and Peorian intervals, may not have been as warm as the present.

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#### THE OXYGEN CONSUMPTION OF NERVE DURING ACTIVITY

THE recent article in this journal by Professor Winterstein<sup>1</sup> dealing with the above question has just come to my attention. The increase in oxygen consumption, over its resting value, of a nerve, stimulated by induction shocks, has been regularly interpreted as measuring the active metabolism of conduction. Winterstein presents reasons for considering this excess oxygen as the result largely or entirely of a local response to an artificial stimulus, and therefore unrelated to the normal events of conduction. Some of the points he makes are as follows. (1) When the region of the nerve actually stimulated is in the

respiration chamber, the resting oxygen consumption is increased up to 400 per cent.; but when the excited region is excluded and the conducting trunk studied only a 14 per cent. increase or, in his own experiments, no increase is observed. (2) The extra oxygen consumption of the frog's spinal cord is much greater on direct electrical stimulation than when excited *via* a nerve—even when strychnized. (3) After stimulation of a dog-fish spinal cord no longer evoked muscular responses an excess oxygen consumption was still to be obtained. (4) The oxygen consumption of a snake's vagus nerve was not changed when the central and peripheral connections were severed, although normal spontaneously passing impulses were abolished.

It may not be amiss to point out here some possible answers to these points other than that suggested by Winterstein, as well as to indicate some of the important evidence that can not, apparently, be reconciled with his view. (1) It seems unwise to express the oxygen consumption of activity as a percentage of the resting, since much evidence indicates that the variables are independent. The resting metabolism is largely a carbohydrate oxidation or glycolysis, the active surely not. The former depends on nerve fibers, sheath, connective tissue, etc., while the latter is presumably limited to the axones themselves; and these structural elements vary widely from species to species. As a matter of fact, for dog-fish lateral line nerve the percentage increase in respiration on activity as determined by Parker, stimulating outside the experimental chamber, and Fenn, stimulating within, was almost identical. For the American green frog, Parker found a 14 per cent. increase; Fenn a 26 per cent. increase, and I (1930),<sup>2</sup> also stimulating within the chamber, a 35 per cent. increase. For the European frog I found for continuous stimulation a 100 per cent., for intermittent stimulation a 300–400 per cent. increase. The absolute increase in all cases, allowing for temperature, etc., was roughly the same—the values obtained when the stimulus occurred inside the chamber were *not* higher than when it was excluded.

(2) It is doubtful if even on direct electrical stimulation of the spinal cord all nerve cells are activated, and also glia and other cells may be stimulated or injured. The increased oxygen consumption is determined by the sum of all. Stimulation of an afferent nerve not only will fail to affect non-nervous tissues, but also there is ample evidence that, even after strychnine, such afferent impulses will not reach all cells and of those reached not all will be excited—some are actually inhibited. The reflexly evoked

<sup>1</sup> H. Winterstein, *SCIENCE*, 71: 641, 1930.

<sup>2</sup> R. W. Gerard, *Proc. Soc. Exp. Biol. and Med.*, 27: 1052, 1930.

activity could hardly equal the effects produced by passing a current through the cord itself.

(3) Similarly with the dog-fish cord. Absence of external response does not guarantee absence of conduction and responses all through the cord itself. There is another point in connection with (2) and (3) that will be returned to.

(4) The number of fiber-impulses normally passing along a vagus nerve is unknown, but compared with those evoked by tetanization with maximal stimuli is probably insignificant. The impulses continuously passing to skeletal muscle to maintain tone are, as judged by tension, less than 1 per cent. of the maximum motor impulses possible (neglecting afferent fibers). The elimination of such an amount of activity in the vagus could not be detected.

In favor of the accepted view of the functional significance of the extra oxygen consumption of activity may be mentioned the following: (a) The extra oxygen consumption agrees quite well with the extra heat production of frog nerve—although in heat measurements the region stimulated is several centimeters removed from that observed, and also the observed heat production is abolished when the nerve is blocked between the region stimulated and that lying on the thermopile. (b) Extra heat production and respiration last 10 to 30 minutes after all stimulation has ceased. (c) During equilibration, and in other conditions, the extra heat production, oxygen consumption and action potentials vary concomitantly. (d) These same changes reach a maximum with increasing stimulus strength and then do not further increase until much stronger shocks are used. This is true for oxygen consumption when the stimulus is applied within the chamber, *i.e.*, oxygen consumption does not parallel shock strength.

A control experiment to fully test the stimulus effect was reported in my initial paper (1927)<sup>3</sup> on this subject, and has recently been repeated by Mr. Chang, working with me. Two sets of nerves of the same frogs are mounted in the usual way on the electrodes of the two chambers of a differential manometer. On one side, the nerve trunks are cut a few millimeters from the electrodes, leaving the ends in place. On this side, then, the effect of stimulation with very little conduction is obtained, on the other stimulation plus full conduction. In two trials the increased oxygen consumption on stimulation with maximal shocks was 50 times greater on the intact side than on the cut one.

A final word on the effects of stimulation. Conduction involves, of course, successive stimulation of regions along the nerve. A stimulus, in order to just

initiate this reaction, need only reach a threshold value over a microscopic region. As an electric current is increased in strength it spreads over a larger region and is able to cause excitation over this region, aside from conduction. When still more intense, electrolysis effects must begin to become serious and many secondary oxidations ensue. It must certainly be possible with strong electrical stimuli to obtain an increased oxygen consumption quite independently of the physiological response of the tissue. But with just adequate stimuli the local effect would seem, from the evidence presented, to be negligible. Professor Winterstein's failure to detect an increased oxygen consumption during activity when the stimulation took place outside the chamber must be explained, I believe, by injury to the nerve or inadequate sensitivity of the apparatus.

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#### SETIGEROUS CYSTS IN THE EARTHWORM

In the course of the routine dissection in the laboratory of *Lumbrius*, a very curious abnormality was discovered which was quite new to the laboratory staff and whose significance is not yet evident. This note is made in order to call it to the attention of others who may have observed it or who may be able to enlighten the author.

In the posterior portion of the specimen, which was of large size, obtained through the General Biological Supply House, in the segments from the eighth to the twenty-second from the posterior extremity, at least thirty-four conspicuous cysts were discovered. They were of oval form and of dirty, yellowish brown to dark purplish brown color and seemed to be lying loose in the coelom. Under ordinary low power there was no evident broken edge to indicate an attachment to the body wall, and some of the cysts dropped out simply on inverting the split end of the worm under water. In some segments as many as three cysts occurred.

Upon teasing the cysts with dissecting needles, it was found that they contained large numbers of setae of varying sizes. Some of the setae were nearly 1.5 mm in length, others only about .5 mm. Upwards of forty setae occurred in a single cyst. In one large cyst, the setae lay for the most part closely packed together approximately parallel to the long axis of the cyst. In most cases the setae were perfectly normal in form and appearance, but occasionally the chitin appeared to be irregularly split and fissured. This may have been an artifact. Besides the setae, in many of the cysts there were numerous nematodes of undetermined species. Usually there were as many as a dozen in a single cyst. Besides the adult worms

<sup>3</sup> R. W. Gerard, *Am. Journ. Physiol.*, 82: 381, 1927.