

of trains of impulses in these units. At shorter intervals the recovery processes of the neuron limit the generation of impulses, preventing the distribution from being truly exponential.

The highly irregular character of the discharge patterns observed in response to stimulation with pure tones, and the general similarity of the interval distributions for most units, appears to preclude any simple interpretation of the coding of tone frequencies by the pattern of impulses carried by individual neurons.

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Search for Evidence of Axial Current Flow in Peripheral Nerves of Salamander

Abstract. The demonstrated association of the d-c bioelectric field with central nervous system elements implies the longitudinal flow of charge carriers within that system. Transverse d-c voltages, attributed to the Hall effect, have been obtained from the extremities of intact salamanders under circumstances suggesting such electric current. These voltages disappeared after nerve section, and their magnitude was related to the depth of anesthesia.

The d-c or steady-state, bioelectric field has been studied extensively (1), and has been found to correlate with growth (2), tissue repair (3), tumor formation (4), cephalocaudal relationships (5), sleep state in man (6), and human behavior (7).

Recently, precision determinations have shown that this bioelectric field is a complex one, with multiple sources

and sinks bearing a close spatial relationship to the anatomical arrangement of the central nervous system (8). This observation led to the theory that the d-c field is generated within and distributed by elements of this system and that it might further represent a primitive data transmission mechanism of neural or neural-related tissue. This theory is at variance with the views which hold that the d-c field is generated by the sum total of electrical activity of all of the cells of the organism and that it possesses no specific organization other than cephalocaudal polarity (9). Implicit in the thesis is the necessity for longitudinal movement of electrical current carriers within the neural structures, and demonstration of such a phenomenon would be necessary for further substantiation. The Hall effect (generation of a potential gradient at 90° to the direction of current flow in the presence of a steady-state magnetic field, oriented at 90° to the direction of current flow and also at 90° to the potential gradient) was selected as evidence to be looked for in support of the hypothesis of axial current flow.

Adult salamanders (*Triturus viridescens*) were used since the d-c field has been completely mapped in this animal. Intact extremities were utilized rather than nerve fibers dissected free to prevent interference from currents of injury. The nerves, however, can be completely severed by fairly simple surgical approaches at a distance far enough away from the recording electrodes to avoid pickup of injury currents. Electrodes were silver-silver chloride, saline-filled, with thin, terminal, cotton wicks. The magnetic flux was obtained from a 7000-gauss permanent magnet with a 3/8-in. air gap, mounted on a movable nonmagnetic support. The electrode contacts were placed just proximal to the elbow joint in such fashion that a line joining both contacts would be 90° to the long axis of the limb and oriented in a cephalocaudal direction.

The magnet was so arranged that, when it was swung into position, the flux field completely encompassed the areas of electrode contact, with the field direction oriented 90° to the line joining the electrodes. Movement of the magnet was without mechanical vibration, and care was taken to insure that no portion of the magnet or its support came into direct contact with the animal. Potentials were amplified by a chopper type direct-coupled preamplifier and a d-c power amplifier. All determinations were carried out in a double-

walled Faraday cage, and the experimental setup was as shown diagrammatically in Fig. 1.

The electrodes alone making contact through a drop of saline demonstrated a steady potential of 25 μ v. No change in this potential was obtained with the application of the magnetic field other than the voltage transients associated with movement of the field in and out of position (Fig. 2A). These transients averaged about 4 sec in duration. In the animal experiments, once the magnet was swung into position it was left stationary for from 20 to 60 sec, a time more than sufficient to permit decay of the transients.

In all 24 salamanders tested, transverse d-c voltages of from 10 to 150 μ v were obtained during the period of steady-state magnetic field application. Removal of the magnetic field brought about a return to the original base line

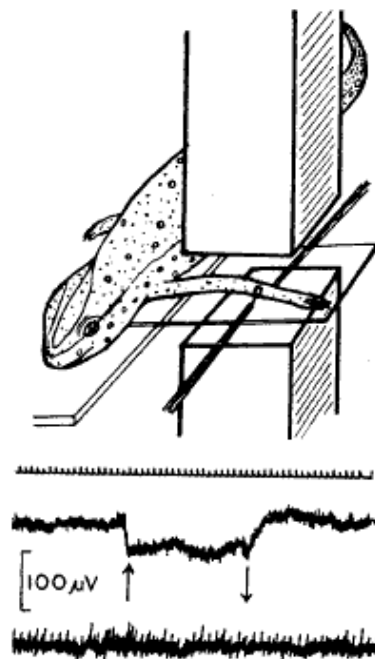


Fig. 1. (Top) Schematic view of the experimental apparatus with the magnet poles swung into place. All portions of the apparatus are made of nonmagnetic materials. The long axis of the limb, the direction of the magnetic flux field, and the inter-electrode line are all at 90° to each other. (Bottom) Top trace is a time marker with 1-sec intervals. The second trace is a typical Hall voltage, the transients of opposite sign indicating magnet movement. The arrow pointing up indicates movement of the magnet into position; pointing down indicates movement out of position. The lower trace is the electrocardiogram measured from precordium to the right extremity—the rate here is about 50 per minute with irregularities.

d-c voltage. The transverse voltages were steady for as long as the magnet remained in place and showed no fluctuation synchronous with blood flow pulsations (Fig. 1). The amplitude of the voltages obtained appeared to be related to the level of anesthesia, being absent during deep anesthesia and increasing in amplitude as recovery occurred. During light anesthesia, two types of slow wave forms appeared in the voltage record. One had a period of approximately 1.25 sec, the other of 15 to 20 sec. These were usually of sufficient magnitude to mask the shifts in the base line unless their magnitude was quite high (Fig. 2C). The clearest records were obtained during moderate anesthesia prior to the appearance of the slow wave forms (Fig. 2B).

In five of the specimens, the brachial plexus was exposed through an anterior incision on the thorax, and it was found possible to section all of the nerves

without interfering with the blood supply to the extremity. (Blood flow in the digital vessels is easily visualized with a magnification of 20 and was not markedly altered by this procedure.) After the nerve section, no transverse voltages could be obtained in response to an applied magnetic field in any stage of anesthesia, and the transverse voltages of the contralateral, nondenervated limb declined markedly. The normal d-c field voltages (longitudinal) in the intact animal average from 10 to 30 mv between the brachial area of the spine and the extremity tip, with the tip negative. After brachial plexus sectioning, these voltages drop to about 10 percent of their normal value, and frequently the voltages on the contralateral limb decrease by 50 percent or more.

In the intact animal, sectioning of the spinal cord at the level of the lower medulla results in a marked drop in the d-c field voltages in both forelimbs to about 10 percent of their normal value. In this case the transverse voltages also promptly disappeared in the same extremities along with the slow wave pattern.

Since a stationary magnetic field can have an effect only on charge carriers moving at right angles to the field, then the transverse voltages obtained are interpreted as Hall voltages, resulting from longitudinal charge carrier movement in the extremity. The independence of the observed voltages from the pulse rate, and the disappearance of these voltages after nerve section alone, indicate that the charge carrier flow is related to the peripheral nerves and that blood flow is not the parameter being measured. That the observed effect is dependent upon the functional state of the nervous system is further evidenced by the amplitude changes with different levels of anesthesia and by the change in the transverse voltages in the contralateral limb after nerve section on the opposite side. The action potential spike is presumably associated with ion movements in a direction transverse to the long axis of the axon. This direction of movement, the low mobility of ions, plus the steady state of the observed transverse voltages mediate against this activity being a factor in the production of the phenomenon.

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Variable Expressivity of a Mutant Gene in Leopard Frog

Abstract. The genetic distinction between the nonspotted, or burnsi, mutant and the common-spotted, wild-type leopard frog is not simply unifactorial. The burnsi phenotype is a manifestation of genic interaction between a major pigmentary locus and a complex of modifiers (minor genes with small effects).

The disciplines of genetics and embryology converge in the search for the causality of development and differentiation. Regrettably, the paucity of genetical data in amphibians contrasts sharply with the wealth of embryological knowledge of the group. Whatever genetical information has accumulated has been admirably used to study the role of genes in development. Witness, for example, the biochemical analysis by Baker (1) of the nonspotted (burnsi) mutant of the common leopard frog (*Rana pipiens*) and the nuclear transplantation experiments by McKinnell (2) involving the mottled (kandyohi) deviant of the common leopard frog. Each of these variant pigmentary traits is seemingly based upon a simple mode of inheritance (3, 4). However, it should be recognized that more intensive analyses would undoubtedly reveal complexities in the mode of transmission of the traits, which, in turn, would complicate embryological findings dependent upon the genetical data. This is attested by the results of a protracted investigation on the inheritance of the nonspotted (burnsi) pattern, which was heretofore thought to differ from the wild-type pattern by a single dominant gene.

J. A. Moore (3) demonstrated that the burnsi gene (designated *B*) exerts a dominance over the wild-type or



Fig. 2. Transverse voltages obtained under the conditions indicated in each case. Arrows indicate magnet movement as in Fig. 1. (A) Voltage measured from the electrodes alone with and without magnetic field. No d-c shift is observed ($50 \mu\text{v}/\text{cm}$). (B) Example of the usual Hall voltage found in moderate anesthesia ($100 \mu\text{v}/\text{cm}$). (C) Example of high magnitude Hall voltage noted during recovery phase of anesthesia; the two types of slow waves are clearly visible ($100 \mu\text{v}/\text{cm}$). (D) Transverse voltage measurements after nerve section; no evident Hall effect is visible ($50 \mu\text{v}/\text{cm}$). (E) Voltage after section of cord at medulla ($50 \mu\text{v}/\text{cm}$).