Applicability of Hodgkin-Huxley Model to Experimental Data from the Giant Axon of Lobster

Abstract. This mathematical model of the squid giant axon has been modified to duplicate action potentials of lobster axons. An increase of the leakage potential (V_L) by 22.6 millivolts increases the amplitudes of the resting potential, action potential and subthreshold response, and eliminates the undershoot.

Although the form and magnitude of action potentials computed from the Hodgkin-Huxley model agree well with experimental data for the squid (*1*), they differ somewhat from action potentials recorded intracellularly from the lobster giant axon (*2*) or the crayfish giant axon (*3*). The Hodgkin-Huxley model has an action potential 20 to 25 mv too low to fit the data for crustaceans, and both the shape of the falling phase of the action potential and the magnitude of the subthreshold response are different. In the model (Fig. 1*A*) and in experimental data for excised squid axon, there is an "undershoot" immediately following the action potential—a transient hyperpolarization of approximately 12 mv (*4*). Such an undershoot is not normally present in the lobster or crayfish action potentials. The latter return either directly to the resting potential, or, in some cases, more slowly, with a "delayed repolarization." Recent experiments (*5*) indicate that the magnitude of the subthreshold response which just fails to initiate an action potential is considerably larger in the lobster axon than that shown in the mathematical model. Finally, the 60 mv absolute resting potential of squid axons (*6*) is 10 to 15 mv lower than the values for crustaceans.

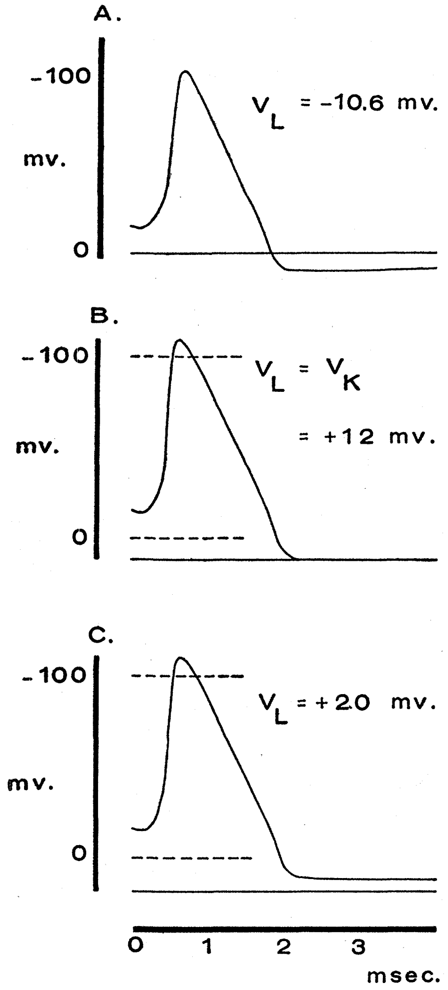
Analog computations (*7*) were made with a modified Hodgkin-Huxley model in order to duplicate the experimental data for crustaceans. The experimental action potentials were propagated normally, while a space clamp with controlled current was assumed for the theoretical ones. However, the latter nonpropagated curves closely resemble theoretical propagated action potentials, which are much more difficult to compute (*1, 8*).

In the normal Hodgkin-Huxley model, in addition to the sodium and potassium currents, a third "leakage" current is carried by other (unspecified) ions, and is represented by a leakage potential (V_L) in series with a constant leakage conductance. In the standard equations, the resting potential is taken as zero, V_L is -10.6 mv, and the potassium potential (V_K) is $+12$ mv. After excitation, during the undershoot, V momentarily approaches V_K before returning to zero.

Figure 1*B* shows an analog computer solution to the equations with V_L changed so as to equal V_K. In this case the new resting potential nearly equals V_K (an increase of 12 mv), and after the action potential, V returns immediately to this value, with no undershoot or delayed repolarization. The total action potential relative to the resting level is increased by about 20 mv, 8 mv of which results from a change in peak potential. The dashed lines indicate the original levels of resting and peak potentials. This computed action potential agrees very well with experimental data from the lobster and crayfish axons with respect to the magnitudes of the resting potential and action potential, and the shape of the falling phase.

The delayed repolarization, which is sometimes seen in the crustacean axons, can be mimicked by a further change in V_L to $+20$ mv (Fig. 1*C*). An eventual return to the resting potential occurs, but it is too slow to show in this figure. There are also further increases in the magnitudes of the action and resting potentials.

A change in V_L also produces changes in the magnitudes of subthreshold responses which more closely agree with reported experimental values (*5*) than do those from the original equations. In the lobster axon, the reported mean value of the maximum subthreshold response is 23 mv, a value which closely agrees with that computed for $V_L = +20$ mv (Fig. 2*B*). Experiments with the lobster giant axon in low sodium show that this treatment produces an increase in the magnitude of the subthreshold response and in its rate of fall. This effect appears in Fig. 2*C*, where the sodium potential (V_{Na}) has been decreased, to mimic experimental reduction of external sodium.



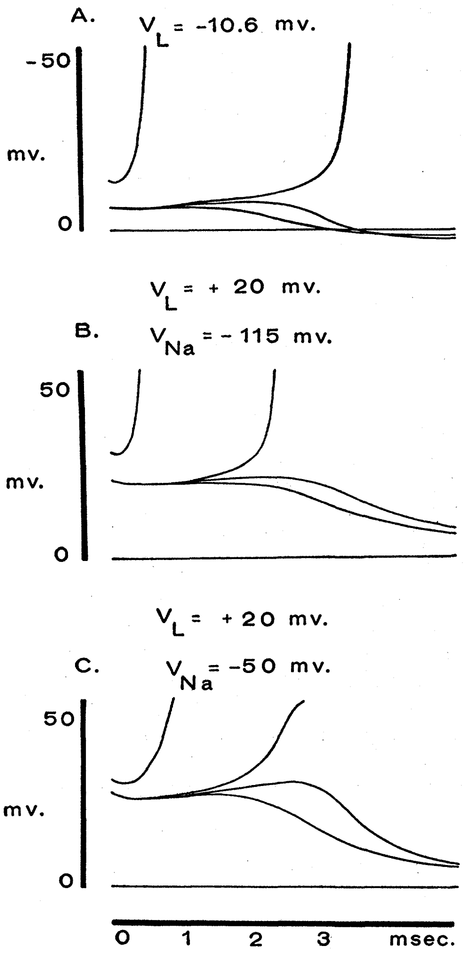


Fig. 1 (left). Analog computer solutions of the Hodgkin-Huxley equations, with temperature coefficients set for 12°C. *A*, Standard equations, with the leakage potential (V_L) at its normal value of -10.6 mv. *B*, V_L equal to the potassium potential ($V_K = +12$ mv). *C*, $V_L = +20$ mv. The distance between dashed lines in *B* and *C* shows the original height of the action potential as computed in *A*. Fig. 2 (right). Analog computer solutions of the Hodgkin-Huxley equations, with stimuli just above and below threshold. *A*, Standard equations, $V_L = -10.6$ mv. *B*, $V_L = +20$ mv. Sodium potential (V_{Na}) at normal value of -115 mv. *C*, $V_L = +20$ mv; $V_{Na} = -50$ mv. The zero millivolt scales in *B* and *C* have been shifted to a new resting level, which differs from that in *A* by 18 mv.

If instead of changing V_L, the leakage *conductance* is changed to zero, the theoretical resting potential changes from zero nearly to V_K, as in Fig. 1*B*. Low signal levels in the analog computer, however, prevented accurate computation of this alternative modification.

We conclude that a change in one parameter (V_L) of the Hodgkin-Huxley equations is sufficient to describe experimental potential curves of lobster and crayfish giant axons (*8*, *9*).

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References and Notes

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4. In action potentials recorded in vivo from the squid, the undershoot decays very slowly and may be entirely absent in the normal axon (J. W. Moore and K. S. Cole, *J. Gen. Physiol.*, in press).
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9. This study was supported in part by research grant B-1748 from the National Institute of Neurological Diseases and Blindness, National Institutes of Health, U.S. Public Health Service. We thank Dr. W. Knox Chandler for his assistance in obtaining some of the analog computer solutions.

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Prehistoric Copper Objects from Western Mexico

Abstract. A series of Pre-Columbian copper artifacts from Nayarit, Mexico, is analyzed. Evidence of deliberate alloys is negative, but the specimens are important as early examples of metal working in Mesoamerica.

Recent excavations in the state of Nayarit on the Pacific coast of Mexico have yielded a large number of objects made of copper. The objects, over 100 in all, come from three different prehistoric sites in the vicinity of Santiago Ixcuintla, near the settlements of Amapa, Coamiles, and Peñitas. All the artifacts, which include awls, eyed needles, bells, small sheets or "slugs" of metal, and a finger ring, were recovered in controlled excavations made under the auspices of the University of California, Los Angeles, under permit from the Instituto Nacional de Antropologia e Historia, Mexico.

Table 1. Pre-Columbian copper artifacts from Nayarit, Mexico. Chemical analysis of samples 739, 342, 455, and 601 was carried out by Dave Ross (U.C.L.A.). The specimens were examined spectroscopically before analysis; Cu was determined electrolytically, Ni by precipitation with dimethylglyoxime, and As through distillation as the trichloride followed by titration with iodide. These pieces were cleaned of surface corrosion products before analysis. Sample 1256 was examined by x-ray fluorescence through the courtesy of Larry Knight (U.C.L.A.). Nothing but Cu was recorded. Samples 1246, 3120, and 3310 were analyzed by high mass spectrometer through the courtesy of the California Research Corporation. These samples were badly corroded, and surface encrustation was not removed; hence a high reading for corrosion products was obtained. +, Trace; −, absent.

No.	Site	Object	Size (cm)	Percentage of component by weight						
				Cu	Fe	Ni	As	W	Ag	Dirt and corrosion products*
				Chemical analysis						
739	Peñitas	Celt	14.2 × 4.5 × 1.6	98.35	+	+	1.50	−	−	
342	Peñitas	Tip of awl	0.19 (diam.)	99.42	−	−	−	+	−	
455	Peñitas	Sheet copper	1 × 1	+	†	†	†	†		All
601	Coamiles	Needle with eye	11 × 0.2	99.63	−	+	−	+	−	
				X-ray fluorescence						
1256	Amapa	Oval slug	6.4 × 3.6 × 0.3	98+						
				Mass spectrometry						
1246	Amapa	Sheet copper	4.0 × 3.5 × 0.1	70.33	0.34	−	−	−	0.10	29.23
3120	Amapa	Bell	1.5 (diam.)	33.94	0.96	−	−	−	+	65.10
3310	Amapa	Bell	1.0 (diam.)	72.20	0.57	−	−	−	0.17	27.06

*Si, O, Na, Mg, Al. † Could not be analyzed.

Copper artifacts have also been reported from Sinaloa (*1*), and as far north as Arizona and New Mexico (*2*), where well over 100 objects have been found in scattered archeological sites. The Arizona–New Mexico finds, formerly believed to have been manufactured locally, are now generally considered to be trade pieces from Mexico since they are identical in form and manufacture to Mexican specimens. The location of the prehistoric copper mines is not known, although they were no doubt somewhere in the Sierra Madre Occidental, possibly in the state of Durango.

The Nayarit specimens are of interest because many of them were found in mounds of domestic refuse, showing that copper artifacts were in common use. The dating also appears to indicate that the use of copper is more ancient on the west coast than in central Mexico, suggesting that knowledge of metallurgy may have originated in the west coast area.

The chronology is uncertain, but copper artifacts from Nayarit are found associated with pottery that is presumably Late Classic and Early Post-Classic in date—something to be equated with the Mazapan horizon in central Mexico. According to the dating system based on the Spinden correlation, the bulk of the copper objects were made between A.D. 700 and A.D. 1100. Copper objects seem to have reached southern Arizona by A.D. 900 and northern New Mexico by A.D. 1000 or 1100; it would not be surprising if they originated in western Mexico at a somewhat earlier time. This system yields a consistent if highly speculative chronology, since we do not have firm dates for the first appearance of copper in any of the regions mentioned.

A couple of broken copper artifacts from Nayarit showed a yellowish color, suggesting the possibility of alloys with other metals. Deliberate alloys are not generally found in Mesoamerica, and the most important technological alloy, bronze, although known in the Andean area, has not so far been found in Mexico. Accordingly, several examples were analyzed; the results (obtained at different times by different methods) are given in Table 1. All of the objects analyzed proved to be essentially pure copper. The only exceptional piece is a copper celt (No. 739) which contains 1.5 percent arsenic. This is probably too small an amount to permit the sample to be considered a deliberate alloy, although it may be significant that this is the only specimen containing arsenic and is also the only "heavy duty" tool among the objects examined.

In addition to the copper objects mentioned, both gold and silver artifacts (the latter exceedingly rare in Mexico) have been found in Nayarit. Traces of gold leaf were found in the excavations at Amapa, but no specimens have been analyzed.

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