discharge re-strike time by a factor of 10 to 50 (from 5  $\mu$ sec to 50–100  $\mu$ sec). ... " Our experiments suggest a re-strike time that is 10<sup>4</sup> times longer. This estimate of the life of the plasma in our experiments is confirmed by the photographs showing that the plasma in the axis between the electrodes remains luminous for approximately  $4 \times 10^4$  $\mu$ sec after the electric current ceases to flow. We find our observations to be consistent with Uman and Voshall's view (9) that the channel conductivity decay is dependent on the rate of heat transfer. They show that for channels several centimeters in diameter the temperature of the lightning channel will decay sufficiently slowly so that the electrical conductivity will persist for a typical interstroke period of  $4 \times 10$ µsec.

We believe that a possible explanation for the large difference between Wilkins' findings (5) and our own may be that the critical ionization times of 0.5 msec that he observed are characteristic not of the vortex-stabilized discharge, as he has assumed, but rather of small sparklike discharges, similar to our feeder spark, which carry the current flowing from the two electrodes to the vortex-stabilized discharge and which are subjected to a continuous flux of fresh, cold, and un-ionized air.

Several important differences must be taken into account in any attempt to extrapolate our laboratory results to phenomena taking place in the atmosphere. It must be recognized that our electrodes are producing a much higher concentration of metal ions than would be found in the natural atmosphere and that these ions may affect the properties of the plasma. In our laboratory experiments, the potentials of only a few kilovolts were capable of initiating a spark no more than a few centimeters long, so that it was necessary to bring the electrodes almost into contact to initiate the discharge. Once the discharge had been drawn out, even a very brief interruption in the current flow causes a flameout, for the voltage is insufficient to form a new ionized part to bridge the gap between the plasma in the vortex and the electrodes. In the thunderstorm we would not expect this circumstance, for the potentials are such that lightning sparks can jump distances of several kilometers.

Our experiments show that a laboratory vortex can be formed and maintained by electrical heating alone under a variety of conditions. The vortexdischarge combination is a stable, com-

12 JUNE 1970

patible system; the vortex stabilizes the discharge, which in turn drives the vortex by electrical heating. The velocities of a few meters per second and the pressure drop of a fraction of a millibar, which we measure, are of the order of magnitude calculated to result from a heated chimney about 1 m in height. Similar discharges occurring in severe storms, in which the current was of the same order of magnitude but with a voltage three or four orders of magnitude greater than our laboratory discharge and with a heated chimney several kilometers high, might generate and maintain a vortex that had all the properties of a mature tornado.

R. T. RYAN

Arthur D. Little, Inc., 15 Acorn Park, Cambridge, Massachusetts 02140 **B.** VONNEGUT State University of New York, Albany, New York 12203

## **References and Notes**

- A. Abdullah, Mon. Weather Rev. 83, 83 (1955). 1. A.
- 2. B. Vonnegut, J. Geophys. Res. 65, 203 (1960).
- (1964). 5. and L. T. McConnell, ibid. 73, 2559
- (1968). (1968).
  E. R. Rathbun, J. Meteorol. 17, 371 (1960);
  P. A. Silberg, Bull. Amer. Meteorol. Soc. 43, 667 (1962); \_\_\_\_\_\_, J. Atmos. Sci. 23, 202 (1966); J. Carstoiu, C. R. H. Acad. Sci. Ser. B 262, 1263 (1966); S. A. Colgate, Science 157 1421 (1967).
- J. 202, 1203 (1960), S. A. Colgale, Science 157, 1431 (1967).
   J. D. Cobine and D. A. Wilbur, J. Appl. Phys. 22, 835 (1951).
   I. Langmuir, C. G. Found, A. F. Dittmer, Science 60, 392 (1924).
   M. A. Uman and R. E. Voshall, J. Geophys. Page 72, 407 (1966).
- *Res.* **73**, 497 (1968). 10. Supported in part by the Office of Naval Re-
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## Visual Receptor Potential: Modification by Injected Current in the Limulus Lateral Eye

Abstract. The latent period of the light-evoked receptor potential was increased by hyperpolarizing currents injected directly into doubly impaled retinular cells. Indirect hyperpolarization of these cells by injection of hyperpolarizing current into the eccentric cell or other intraommatidial retinular cells either shortened or did not change the latent period. The modification of the latent period may depend upon the direction of current flow across some regions of the membrane system constituting the rhabdomere. The reduction in magnitude of the receptor potential obtained with strong hyperpolarizing currents may also depend upon the direction of current flow. The results support the conclusion that the receptor potential originates in retinular cells within the membrane system of the rhabdomere.

Our study was undertaken to determine whether extrinsic currents injected into retinular cells of the lateral eye of Limulus polyphemus can alter the latent period of the light-evoked receptor potential. Excised lateral eyes of Limulus (1) were impaled with independently manipulated KCl-filled micropipettes. Since we could not check impalement visually and dye-marking was not used, the following criteria had to be met for a cell to qualify as impaled by both electrodes: a change in membrane potential of at least 10 mv for  $4 \times 10^{-9}$ amp of hyperpolarizing current; synchrony and similarity of wave form and magnitude of spontaneous potential fluctuations detected by both electrodes; similarity of wave form and magnitude of the receptor potential; equality of latency of the receptor potential; and equality of the resting membrane potential. Additional qualifications for accept-

ance were stability of the doubly impaled cell for 1 hour or longer, a resting membrane potential of 40 mv or more, and a typical (1) receptor potential. Many double penetrations did not meet these criteria and were either discarded or recorded as combinations of retinular cells or of retinular and eccentric cells, depending on the response characteristics (1, 2), the magnitude of

Table 1. Changes in latent period and membrane potential produced by hyperpolarizing current injected into a doubly impaled retinular cell.

Hyper- polarizing current (na)	Latent period (msec)	Increase in membrane potential (mv)
0-Control	46	0
1.8	52	54
2.2	56	69
3.0	63	119

the membrane potential, and the magnitude of the change in membrane potential produced by the injection of depolarizing current (2). Constant current pulses 0.8 second long were passed through either of the micropipettes and the magnitude of the injected current was determined from the voltage drop across a 100 kilohm resistor between the indifferent bath electrode and ground recorded on the upper trace of the cathode ray oscilloscope (Figs. 1 and 2). The experiments were conducted at room temperature (21° to 23°C). Control latent periods of responses to light pulses ranged from 15 to 50 msec, but were constant for any one preparation.



Fig. 1. Oscillograms illustrating the effect of hyperpolarizing current pulses on the latent period of the receptor potential of a doubly impaled retinular cell stimulated by a light pulse of fixed intensity and duration delivered at the onset of the sweep. Each frame is a double exposure of a dual trace oscillogram, with and without the light stimulus. The trace above each frame number records the magnitude of the 0.8-second hyperpolarizing pulses which began before the initiation of the sweep so that only the last 80 msec of the pulses were recorded. The lower traces in each frame record the intracellular potential of the retinular cell. Frame 1: control response; frames 2, 3, and 4: hyperpolarizing current progressively increased. The inset illustrates diagrammatically an eccentric (E) and a retinular cell (R) impaled with a recording (R) and a currentpassing (1) micropipette.

The effective input resistance of doubly impaled retinular cells ranged from 4.4 to 20 megohm. The lateral eye preparations, previously adapted to the dark, were exposed to brief (10  $\mu$ sec) light flashes at 8-second intervals.

Hyperpolarizing currents injected directly into a retinular cell whose voltage changes were recorded with a second impaling micropipette markedly increased the membrane potential (2) and significantly lengthened the latent period, that is, the time between onset of light stimulus and onset of receptor potential (Fig. 1 and Table 1). We tested whether this increase is attributable to the augmented membrane potential by indirectly hyperpolarizing retinular cells. This was accomplished by injecting currents into eccentric cells and other retinular cells within the same ommatidium (2).

Hyperpolarizing currents injected into eccentric cells significantly hyperpolarized the retinular cells but the latent period either remained constant or shortened (Fig. 2, Table 2). Injection of hyperpolarizing currents into retinular cells other than the one monitored in some cases increased the membrane potential of the monitored cell as much as 83 mv, but it did not affect the latent period. Therefore, hyperpolarization in itself does not account for the increase in latent period.

The fact that increases in latency are graded according to the degree of hyperpolarization over the whole range used seems to rule out any major contribution by an increased membrane resistance of the retinular cell (2). The resistance is increased only over part (0 to  $\sim 20$  mv) of the total range over which the cells can be hyperpolarized. Therefore, the increment in the time constant of the membrane should be constant for hyperpolarizations in excess of 20 mv. Since hyperpolarizing responses (3) did not occur in the cells under consideration, increased membrane resistance of a directly hyperpolarized retinular cell can account for only a fraction of the maximum increase in latency. On the other hand, the variable latencies obtained with indirect hyperpolarization by currents injected into eccentric cells may be adequately accounted for by resistance changes in the complex nonlinear network which the electrotonically coupled intraommatidial retinular and eccentric cells represent (2).

It is unlikely that the observed effects

Table 2. Changes in latent period and membrane potential of a retinular cell hyperpolarized by current injected into the eccentric cell.

Hyper- polarizing current (na)	Latent period (msec)	Increase in membrane potential (mv)
0-Control	37	0
2.8	29	26
5.6	26	76

of extrinsic hyperpolarizing current on the receptor potential can be attributed to  $Cl^-$ , which carries the current for the following reasons: the effectiveness of hyperpolarizing current is dependent on the effective input resistance of the retinular cells rather than on the magnitude of the current pulses; the effects of extrinsic currents are reversible within a second or less; and prolonged treatment with current pulses (4 hours in some cases) produced no apparent change in the control responses of retinular cells.

Within an ommatidium of the lateral



Fig. 2. Oscillograms illustrating the effect of hyperpolarizing current pulses injected into an eccentric cell on the magnitude and latent period of the receptor potential of a retinular cell in the same ommatidium. Each frame is a double exposure, with and without the light stimulus. The sweep and light pulse were triggered simultaneously. Before the recording of frame 3, the lower trace was moved upward. eye of Limulus the eccentric cell is joined to the individual retinular cells by electronic junctions; adjacent retinular cells are similarly joined (2, 4). These findings indicate that all intraommatidial sensory cells are electrically coupled by relatively low-resistance electrotonic junctions. Thus, current injected into any one cell will flow into those cells to which it is coupled by such junctions (2). The rhabdomeric membranes of both retinular and eccentric cells have numerous cylindrical projections, the microvilli, which meet those of neighboring cells to form junctions, some or all of which may have low resistance (5). Consequently, currents transmitted from one cell to others presumably flow across a portion of the membrane system constituting the rhabdom. When a given retinular cell is hyperpolarized either directly or indirectly, the directions of current flow through the high-resistance portion of the retinular cell membrane to the extracellular space must be the same in both cases, since both procedures produce hyperpolarization; but the current flow through the relatively low-resistance electrotonic junctions must be of opposite directions in the two cases. Since hyperpolarizing currents injected directly into a retinular cell increase the latent period whereas hyperpolarizing currents injected into the eccentric cell or another retinular cell either shorten or do not change it, the direction of current flow through the electrotonic junctions in the rhabdom may be significant.

Modification of the latent period of the receptor potential of retinular cells by extrinsic currents is interesting because it demonstrates: (i) that the process which occurs during the latent period, a process which is initiated by light and determines when the receptor potential begins (6), can be influenced by extrinsic currents; (ii) that the direction of the current flow across some regions of the retinular cell membrane determines whether the latent period is increased; and (iii) that the rhabdomere of the retinular cell seems to be the site where the injected extrinsic current affects the latent period of the receptor potential.

Recently Lasansky and Fuortes (7) demonstrated that the microvillar membrane of the leech photoreceptor is the site of an inward, light-evoked current and concluded that the receptor potential originates in this structure. Our re-

12 JUNE 1970

sults also indicate that the rhabdomeric (microvillar) membrane generates the receptor potential. However, our data do not exclude the possibility that nonrhabdomeric membrane may also be actively involved (2, 8, 9).

The reduction in magnitude of the receptor potential produced by relatively strong hyperpolarizing currents may also depend on the direction of current flow through the rhabdomere. When hyperpolarizing currents are injected directly into a monitored retinular cell the magnitude of the receptor potential increases [(2, 8) and Fig. 1]; if the currents are sufficiently strong, the magnitude decreases (8). Such reductions have been observed in seven experiments where it was expressly looked for; in one of these experiments, a hyperpolarizing current of 4.5 na increased the membrane potential by 64 my and virtually suppressed the receptor potential. Yet, indirect hyperpolarization of retinular cells does not reduce the amplitude of the receptor potential (Fig. 2).

Our results support the conclusion that the receptor potential of the lateral eye of Limulus originates in retinular cells (2, 9), that the rhabdomeric membrane system (or a part of this system) generates the receptor potential, and that the reaction or reactions occurring during the latent period may be influenced by intracellularly injected extrinsic currents.

V. J. WULFF, C. MENDEZ Masonic Medical Research Laboratory, Utica, New York 13501

## **References and Notes**

- 1. M. E. Behrens and V. J. Wulff, J. Gen. Phy-
- M. D. Bendrifs and V. St. Hum, et Com. Phys. soil. 48, 1081 (1965).
   T. G. Smith and F. Baumann, Progress in Brain Research (Elsevier, Amsterdam, 1969), p. 313. 3. H. P. Reuben, R. Werman, H. Grundfest,

- H. P. Reuben, R. Werman, H. Grundfest, J. Gen. Physiol. 45, 243 (1961).
   A. Borsellino, M. G. F. Fuortes, T. G. Smith, Cold Spring Harbor Symp. Quant. Biol. 30, 429 (1965); T. G. Smith, F. Baumann, M. G. F. Fuortes, Science 147, 1446 (1965).
   W. H. Miller, Ann. N.Y. Acad. Sci. 74, 204 (1958); A. Lasansky, J. Cell. Biol. 33, 365 (1967); W. H. Fahrenbach, Z. Zellforsch. 93, 451 (1969); R. Whitehead and R. Purple, personal communication. personal communication.
- bersonal communication.
  c. S. Hecht, J. Gen. Physiol. 1, 657 (1919); V. J. Wulff, W. J. Fry, F. A. Linde, J. Cell. Comp. Physiol. 45, 247 (1955).
  A. Lasansky and M. G. F. Fuortes, J. Cell. Physical Science (1997).
- *Biol.* 42, 241 (1969). R. Kikuchi and M. Tazawa, in *Electrical*
- K. Kikuchi and M. Tazawa, in *Electrical Activity of Single Cells* (Igakushoin, Tokyo, 1960), p. 25; R. Kikuchi, K. Naito, I. Tanaka, *J. Physiol.* 161, 319 (1962).
   T. H. Waterman and C. A. G. Wiersma, *J. Exp. Zool.* 126, 59 (1954); T. Tomita, *Jap. J. Physiol.* 6, 327 (1956).
   Portiv currented by NHL creat 5, 201 NP.
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## Carbon-13 and Oxygen-18 in Dinosaur, Crocodile, and **Bird Eggshells Indicate Environmental Conditions**

Abstract. We have gathered, from the nests of dinosaurs, and living and fossil birds, some evidence of the environment in which these creatures lived. However, our isotope determinations suggest it will be impossible to resolve the problem as to whether the dinosaurs were warm- or cold-blooded from the oxygen and carbon isotope content of their shells.

In 1958 Russell speculated that dinosaurs might have been warm-blooded creatures unable, in their hairless state, to adapt to the changing environment of the late Cretaceous (1). Such speculation is recurrent, but difficult to test.

It occurred to us that a comparison of the oxygen and carbon isotopic composition of dinosaur eggshells from the Cretaceous beds at Shabarakh Usu, Mongolia, and near Aix in southern France, with those of calcareous eggshells of living reptiles (the crocodilians) and birds, living and extinct, might prove the dinosaurs to be more similar to one group than to the other.

Dinosaur eggshell fragments were collected (2) from Rousset near Aix, France, in 1960. We obtained shell fragments from the 1923 collections of the Central Asiatic Expedition near Shabarakh Usu in the Gobi desert, and a crocodile egg from the upper reaches of the Amazon basin in Peru (3). Thinsection and x-ray studies of the shell fragments suggested that the calcite comprising the dinosaur shells was not recrystallized nor contaminated by secondary carbonate and might well have retained its primary isotopic character. Various shell fragments, including those of the extinct giant bird of Madagascar, Aepyornis (4), chickens, ducks,