trophysiological results suggest that this effect may be mediated by way of a direct pathway from the raphe to the SPN's. Although other mechanisms such as disfacilitation or disynaptic inhibition involving a spinal interneuron cannot be definitively excluded, the weights of the combined evidence suggest that the medullary raphe inhibits the SPN's by a direct pathway.

JOHN B. CABOT
J. MARTIN WILD, DAVID H. COHEN
Department of Physiology, School of Medicine, University of Virginia, Charlottesville 22901

References and Notes

1. S. D. Anderson, A. I. Basbaum, H. L. Fields, *Brain Res.* **123,** 363 (1977); A. I. Basbaum, C. H. Clanton, H. L. Fields, *Proc. Natl. Acad. Sci. U.S.A.* **73,** 4685 (1976); J. E. Beall, R. F. Martin, A. E. Applebaum, W. D. Willis, *Brain Res.* **114,** 328 (1976); H. L. Fields, A. I. Basbaum, C. H. Clanton, S. D. Anderson, *ibid.* **126,** 441 (1977); G. Guilbaud, J. L. Oliveras, G. Giesler, Jr., J. M. Besson, *ibid.*, p. 355; W. D. Willis, L. H. Haber, R. F. Martin, *J. Neurophysiol.* **40,** 968 (1977).
2. A. Dahlström and K. Fuxe, *Acta Physiol. Scand. Suppl.* **232,** 1 (1964); *ibid.* **247,** 5 (1965).
3. J. A. Zivin, J. L. Reid, J. M. Saavedra, I. J. Kopin, *Brain Res.* **99,** 293 (1975).
4. A. J. Smolen and L. L. Ross, *ibid.* **139,** 153 (1978).
5. J. R. Adair, B. L. Hamilton, K. A. Scappaticci, C. J. Helke, R. A. Gillis, *ibid.* **128,** 141 (1977); R. S. Alexander, *J. Neurophysiol.* **9,** 205 (1946); J. H. Coote and V. H. Macleod, *J. Physiol. (London)* **241,** 477 (1974); P. M. Gootman and M. I. Cohen, *Am. J. Physiol.* **219,** 897 (1970); *Exp. Brain Res.* **13,** 1 (1971); J. L. Henry and F. R. Calaresu, *ibid.* **20,** 485 (1974); F. Kirchner, A. Sato, H. Weidinger, *Pfluegers Arch.* **326,** 324 (1971); F. Kirchner, I. Wyszogrodski, C. Polosa, *ibid.* **357,** 349 (1975); M. C. Koss and S. C. Wang, *Am. J. Physiol.* **222,** 900 (1972); S. K. Manchanda, R. Bhattarai, U. Nayar, *Indian J. Physiol. Pharmacol.* **19,** 105 (1975); M. Monnier, *Arch. Int. Physiol.* **49,** 455 (1939); R. J. Neumayr, B. D. Hare, D. N. Franz, *Life Sci.* **14,** 793 (1974); J. Pórszász, T. Barankay, J. Szolcsányi, K. Gibiszer-Pórszász, K. Madarász, *Acad. Sci. Hung.* **22,** 29 (1962); D. W. Snyder and G. L. Gebber, *Am. J. Physiol.* **225,** 1129 (1973); S. C. Wang and S. W. Ranson, *J. Comp. Neurol.* **71,** 437 (1939); D. G. Ward and C. G. Gunn, *Brain Res.* **107,** 407 (1976).
6. J. H. Coote and V. H. Macleod, *J. Physiol. (London)* **241,** 453 (1974).
7. A. Carlsson, B. Falck, K. Fuxe, N.-Å. Hillarp, *Acta Physiol. Scand.* **60**, 112 (1964).
8. J. H. LaVail, K. R. Winston, A. Tish, *Brain Res.* **58**, 470 (1973).
9. W. M. Cowan, D I. Gottlieb, A. E. Hendrickson, J. L. Price, T. A. Woolsey, *ibid.* **37**, 21 (1972).
10. R. P. Fink and L. Heimer, *ibid.* **4**, 369 (1967).
11. Nomenclature according to H. J. Karten and W. Hodos, *A Stereotaxic Atlas of the Brain of the Pigeon* (Columba livia) (Johns Hopkins Press, Baltimore, 1967).
12. A cytoarchitectonic analysis of the medullary raphe is not available for the pigeon; however, our preliminary evaluation of the complex suggests an organization similar to that of the cat [E. Taber, A. Brodal, F. Walberg, *J. Comp. Neurol.* **114,** 161 (1960)].
13. H. G. J. M. Kuypers and V. A. Maisky, *Neurosci. Lett.* **1,** 9 (1975).
14. J. B. Cabot and D. H. Cohen, *Brain Res.* **131,** 89 (1977).
15. J. F. Huber, *J. Comp. Neurol.* **65,** 43 (1936); R. L. Macdonald and D. H. Cohen, *ibid.* **140,** 343 (1970); T. Terni, *Arch. Ital. Anat. Embriol.* **20,** 433 (1923).
16. A. I. Basbaum, C. H. Clanton, H. L. Fields, *J. Comp. Neurol.* **178,** 209 (1978).
17. Stimuli were 0.5-msec, cathodal pulses delivered by a constant-current stimulator through No. 00 stainless steel insect pins insulated to give tip exposures of ≃ 100 μm. Electrode localization was verified histologically from 50-μm celloidin sections stained with cresyl echt violet. Threshold was at stimulus intensities of 30 to 60 μA with supramaximal responses at 50 to 100 μA. The SPN's were identified on the basis of collision [I. Darian-Smith, G. Phillips, R. D. Ryan, *J. Physiol. (London)* **168,** 129 (1963)] of a spontaneous discharge with an antidromic discharge elicited by bipolar stimulation of the preganglionic axons in sympathetic ganglion 14 [J. B. Cabot and D. H. Cohen, *Brain Res.* **131,** 73 (1977)]. Recording electrodes were 4*M* NaCl micropipettes with tip resistances of 6 to 10 megohms.
18. The collision test was applied in all cases, and raphe recording sites were verified histologically.
19. Blood pressure and heart rate were recorded by conventional methods (*14*). Stimulating electrodes were located in the raphe while the animals were anesthetized with ether; the animals were allowed to recover for 2 to 2.5 hours before stimulation. Stimulus trains were delivered for 3 or 5 seconds at frequencies of 25, 50, or 100 Hz. Threshold was at intensities of 25 to 50 μA with supramaximal responses at 30 to 100 μA.
20. J. B. Cabot, J. M. Wild, D. H. Cohen, in preparation.
21. D. H. Cohen, in *Limbic and Autonomic Nervous Systems Research*, L. V. DiCara, Ed. (Plenum, New York, 1974), p. 223; D. H. Cohen and D. M. Goff, *Physiol. Psychol.* **6**, 127 (1978).
22. We thank D. Hannum, D. Goff, and N. Richardson for technical assistance. This research was supported by NSF grant BNS-75-20537 to D.H.C. J.B.C. and J.M.W. were supported by fellowships from the Alfred P. Sloan Foundation to the Neuroscience Program at the University of Virginia.

11 April 1978

Zea diploperennis (Gramineae): A New Teosinte from Mexico

Abstract. *A perennial teosinte or "wild maize" endemic to the Cerro de San Miguel, Sierra de Manantlan, Jalisco, Mexico differs from* Zea perennis *by dimorphic rhizomes, robust habit, and a larger number of longer, laxer tassel branches. The fact that it is a diploid (2*n *= 20) has taxonomic and agronomic significance. The seeds are used locally for food.*

Earlier this year, Guzmán (*1*, *2*) reported his remarkable rediscovery of perennial teosinte, thought extinct in the wild since 1921 (*3*), at two sites in southern Jalisco, Mexico. Subsequently, both sites were visited by three of us (H.H.I., J.F.D., and R.G.M.), and specimens, seeds, and rhizomes were collected and initial analyses were made. This report confirms Guzmán's conclusion regarding the Ciudad Guzmán population—that it is, indeed, conspecific with the tetraploid ($2n = 40$) *Zea perennis* (Hitchcock) Reeves and Mangelsdorf, originally discovered in this area by Hitchcock in 1910. However, the plants from the second location, Cerro de San Miguel, though similar in many ways, are a clearly distinct diploid taxon, here described for the first time:

Zea **diploperennis** Iltis, Doebley & Guzmán. **sp. nov.**

Similis a *Zea perennis* sed robustior, culmis 1–2 cm diam., rhizomatibus perennibus dimorphis (gracilioris non nisi 5–15 cm × 5–10 mm, brevioris crassis, tuberosis 1–4 cm × 9–15 mm), uterque cum internodiis brevibus 2–6 mm longis, foliis multo majoribus (40–80 × 4–5 cm), inflorescentiis ♂ cum 3–13 ramis, robustioribus et 6–15 cm longis. Typus: Iltis, Doebley & Guzmán 450.

Robust, erect, maizelike, loosely clump-forming perennial, with five to ten, or more, primary culms from one rhizome system; rhizomes of two intergrading sorts, (i) *cordlike long shoots*, 5 to 15 cm long, 5 to 10 mm in diameter, these with many dense short (2 to 6 mm) internodes, scaleless when mature, usually vertical or strongly ascending and changing abruptly into the much thicker culms, or less often horizontal and producing one to several culms from short lateral shoots, or (ii) *thick and tuberous, ovoid to obovoid short shoots* 1 to 4 cm long, 9 to 15 mm in diameter, each of these produced horizontally from the lowest two or three nodes of the primary culms, clothed when young with triangular, strongly convergent-veined, overlapping, connivent scales, at times growing upward (into a long shoot?) and producing a culm, or sometimes remaining dormant to eventually produce one to four lateral short or long shoots (or both).

Primary culms 10 to 25 dm tall, 1 to 2 cm in diameter, unbranched (or with one to three inconspicuous lateral branches), the nodes, internodes, and leaf sheaths glabrous throughout except for a more or less dense fringe of long hairs on upper sheath margin and auricles of the upper leaves; ligule a thin membrane 1 to 2 mm long, the collar prominent; leaf blades linear-lanceolate, *the major central or lower ones 40 to 80 cm long, 4 to 5 cm wide*, subcordate, glabrous, or subglabrous, except for a few marginal long hairs near base.

Male inflorescences with (2 to) 3 to 13 ± divergent to nodding branches; these 6 to 15 cm long, 12 to 20 mm wide, the central one barely exceeding the others; branching axis 1 to 4 cm long; spikelets in sessile or pedicellate pairs (pedicels 1.5 to 3 mm long), crowded and overlapping (for example, 14 spikelet pairs in 4 cm); the branch internodes short (2 to 6 mm); the branch rachis about 1 mm wide, in cross-section triangular with ciliate edges; spikelets 8.5 to 11.5 mm long, about 3 mm wide; outer glumes very thin and translucent, often purple-

0036-8075/79/0112-0186$00.50/0 Copyright © 1979 AAAS

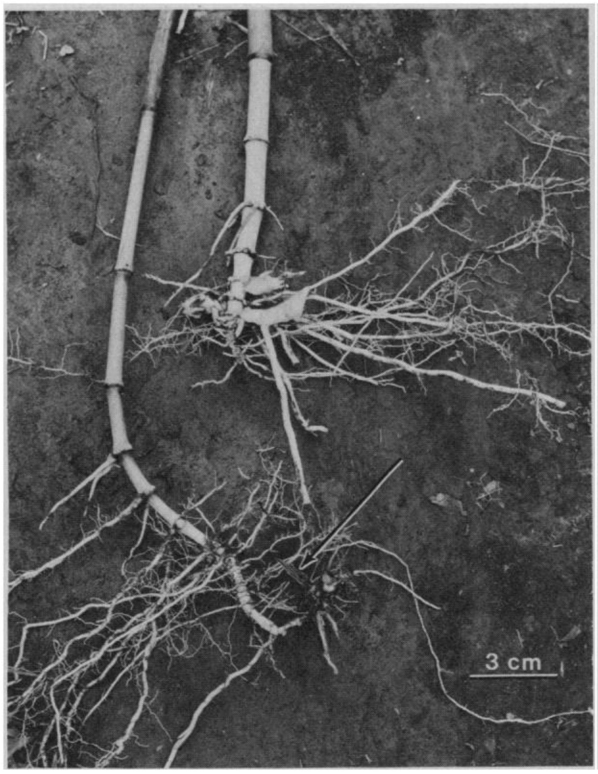

Fig. 1 (left). Root system of *Zea diploperennis*. Left plant showing a cordlike rhizome (note short internodes); right plant has two sectioned tuberous short rhizomes, which are covered with scale leaves; the arrow points to the stump of previous years' culm. Fig. 2 (right). Comparative growth of the two perennial teosinte species in a uniform environment (University of Guadalajara greenhouse), with *Zea perennis* on the left, *Z. diploperennis* on the right, and R. Guzmán M. in the middle. The plants were grown from rhizomes collected in the wild, and were 9 months in cultivation. Plants growing in the wild would be somewhat shorter.

tinged, strongly green-nerved, the nerves usually clustered marginally near the apically ciliate prominent lateral wings; outer glume strongly enclosing inner glume.

Female spikes sessile or often borne on long peduncles, frequently tipped by short male racemes; fruit cases 5 to 10 per spike, trapezoidal-cylindric, 6 to 8.2 mm on the long side, 2.5 to 4.5 mm on the short side, 4 to 5 mm in diameter; when mature light sepia to grayish brown speckled with dark brown or nearly black; weight of 100 mature fruit cases 7.12 g.

Chromosomes number: $2n = 20$; meiosis regular with ten bivalents (*4*).

MEXICO: JALISCO: many, often dense, colonies, mostly among tall grasses and herbs (*Dahlia coccinea*, *Thalictrum*), in deep soft soil, often on edge of (or in) small streams, and sometimes on edge of (but not in) maize fields or in grazed pastures, on what was formerly open *Pinus-Quercus (elliptica?)-Carpinus caroliniana* forest: at base of rocky north-northeast-facing uppermost slopes of Cerro de San Miguel (east end of Sierra de Manantlan), just north of and below saddle (crest) at La Ventana (104°13″W, 19°31′45″N), near an Indian hut surrounded by five gigantic *Yucca (elephantipes?)* trees, 20 km due south of El Chante, 7 km east-northeast of El Durazno (Municipio de Cuautitlán). altitude 2250 to 2400 m, 22 September 1978, H. H. Iltis, R. Guzmán M., J. Doebley, and A. Lasseigne No. 450.

The holotype is in the Herbario de la Universidad de Guadalajara (Zapopán); isotypes (to be distributed) in B, BH, BM, CHAPA, ENCB, F, GH, ILL, K, L, LIL, MEXU, MICH, MO, NA, P, TAES, TEX, UC, US, WIS, XAL (*5*).

Another collection from the same population was distributed as *Zea perennis* [the location data given on this label (see below) and by Guzmán (*1*) are not quite correct]:

> Campos cultivos de maíz cerca del bosque frio de pino, Cerro de la Ventana San Miguel, 15 km al E de la comunidad indigenia de Cuzalapa, Municipio de Cuautitlán, Jalisco, 1700 m alt., 15 December 1977, *R. Guzmán M. 777* [in ARIZ, Universidad Autonoma Guadalajara, Universidad Guadalajara, Zapopán, MICH (*5*)].

This collection included mature seeds which will be distributed with the type material.

Common name: "Chapule," "Maíz Chapule," or "Milpilla."

It is of interest that the local people report grinding up and mixing the kernels with maize for use as food in hard times.

Similar to *Zea perennis*, *Z. diploperennis* differs by its dimorphic rhizomes with much shorter internodes (Fig. 1), those of *Z. perennis* being usually 1 to 3 cm long; by its more open root system which is not densely sod-forming, by the larger number of, and longer and laxer tassel branches (Fig. 2); by wider and longer leaves; and by its considerably more robust habit (Fig. 2).

The implications of this discovery are considerable. (i) Being morphologically primitive, this diploid wild maize could give clues to the evolution of *Zea*, and specifically to the origin of the supposedly autotetraploid *Z. perennis* (*6*), its probable descendant. (ii) Since it is a diploid perennial, and interfertile with maize, as shown by F_1 hybrids, grown from field-collected seeds at the Universidad de Guadalajara, this new species should provide geneticists and maize breeders with a potentially valuable source of germ plasm, and may lead to the development of perennial maize.

Hugh H. Iltis
John F. Doebley
Department of Botany, University of Wisconsin-Madison, Madison 53706
Rafael Guzmán M.
Instituto de Botánica, Apartado 139, Universidad de Guadalajara, Zapopán, Jalisco, Mexico
Batia Pazy
Department of Botany, Hebrew University, Jerusalem, Israel

References and Notes

1. R. Guzmán M., *Boletín Informativo del Instituto de Botánica, Univ. de Guadalajara* **6**, 9 (1978).
2. ———, *Phytologia* **38**, 177 (1978).
3. H. G. Wilkes, *Teosinte: The Closest Relative of Maize* (Bussey Institute, Harvard University, Cambridge, Mass., 1967).
4. Counted by B.P.
5. Symbols for the herbariums are those according to *Index Herbariorum* (International Association of Plant Taxonomists Utrecht, ed. 6, 1974): B, Berlin Botanical Gardens, Berlin Dahlem; BH, Bailey Hortorium, Cornell University; BM, British Museum of Natural History, London; CHAPA, College of Agriculture, Chapingo, Mexico; F, Chicago Natural History Museum; GH, Gray Herbarium, Harvard University; ENCB, Polytechnic Institute of Mexico City; ILL, University of Illinois, Urbana; K, Kew Gardens, London; L, Leiden, Holland; LIL, Instituto Lillo, Tucuman, Argentina; MEXU, National Herbarium of Mexico; MICH, University of Michigan; MO, Missouri Botanical Gardens, St. Louis; NA, National Arboretum, Washington, D.C.; P, Natural History Museum, Paris; TAES, Texas A & M, College Station; TEX, University of Texas, Austin; UC, University of California, Berkeley; US, U.S. National Herbarium, Smithsonian Institution, Washington, D.C.; WIS, University of Wisconsin, Madison; XAL, Institute of Biotic Resources, Xalapa, Mexico.
6. D. L. Shaver, *Caryologia* **15**, 43 (1962).
7. We thank Dr. Luz Puga who provided the critical link in the chain of events leading to this discovery. Supported by grants from the National Science Foundation (BM S74-21861), the Research Committee of the Graduate School, the Davis Fund, and the Allen Fund, Department of Botany, University of Wisconsin-Madison.

3 November 1978

Cerebral Glucose Utilization: Local Changes During and After Recovery from Spreading Cortical Depression

Abstract. *Cerebral glucose utilization is markedly increased in most areas of the cerebral cortex and reduced in many subcortical structures during spreading cortical depression. During recovery, cortical glucose utilization is still elevated, but the increased metabolic activity is distributed in columns running perpendicularly through the cortex.*

Spreading cortical depression, a phenomenon first described by Leão in 1944 (*1*), remains a puzzling and still poorly understood response of the cerebral cortex to a variety of noxious stimuli. It can be elicited by mechanical, electrical, thermal, and chemical stimuli (*2*) and is characterized by a spread of transient intense neuronal activity followed by depression in all directions from the site of initiation at a rate of 2 to 5 mm/min (*2*). This rate of spread is similar to that seen in the Jacksonian march of convulsions or the development of the scotomata of migraine in man (*2, 3*). The electrophysiological changes consist of depolarization and decreased electrical activity of neuronal units, depression of amplitude of the electroencephalogram, increased electrical impedance, and a negative shift in the d-c potential of the affected cortex (*2*). There is also evidence of chemical changes in the depressed cortex, for instance, a release of K^+ and an increase in extracellular K^+ (*4*), decreased cortical pO_2 (*2*), decreased concentrations of glycogen, glucose, and phosphocreatine (*5*), and increased concentrations of inorganic phosphate and lactic acid (*5*). Some of these chemical changes are suggestive of increased energy metabolism, but measurements of cerebral cortical energy metabolism in spreading cortical depression have not been reported. We have, therefore, employed the [^{14}C]deoxyglucose method (*6*) to determine the regional rates of glucose utilization within the brain during and after the evocation of spreading cortical depression.

The experiments were performed on normal male Sprague-Dawley rats weighing between 370 and 410 g. The procedure for measuring local cerebral glucose utilization has been described (*6*). Briefly, polyethylene catheters were inserted into a femoral artery and vein under light halothane–nitrous oxide anesthesia, and the animal was then restrained by application of a loose-fitting abdominal-pelvic plaster cast. Holes, approximately 2 to 3 mm in diameter, were drilled through the skull over the occipitoparietal cortex on both sides of the head to expose the dura, which was then kept covered with mineral oil. At least 2 hours were then allowed for complete recovery of the animal from the effects of anesthesia.

In one group of animals spreading cortical depression was induced in one cerebral hemisphere by the application of a filter paper disk soaked in 3*M* or 5*M* KCl to the exposed dura on that side. Another disk soaked in 0.15*M*, 3*M*, or 5*M* NaCl was applied to the exposed dura on the opposite or control side. Both disks were replaced with freshly soaked disks at 15- to 20-minute intervals until the end of the experimental procedure. The animals so treated remained conscious, but spreading cortical depression appeared within 3 to 5 minutes after application of the KCl disks and was manifested by a marked hemiparesis and hemianesthesia on the side of the body contralateral to the side of KCl application. Measurement of local cerebral glucose utilization was initiated 15 to 20 minutes after the first application of the KCl and NaCl disks by the administration of a pulse of 50 μCi of 2-deoxy-D-[1 $-$ ^{14}C]glucose (specific activity, 50 to 55 μCi/μmole) via the femoral venous catheter. Arterial blood samples were rapidly drawn immediately after the pulse and at timed intervals for 45 minutes. The blood samples were immediately centrifuged to separate the red cells, and the plasma samples were stored on ice until subsequently analyzed for glucose and [^{14}C]deoxyglucose concentrations as described (*6*). At the end of the 45-minute period, the animal was decapitated, and the brain was removed as rapidly as possible, frozen in Freon XII chilled to −60° to −70°C with liquid nitrogen, sectioned, and subjected to quantitative autoradiography as described (*6*). Local cerebral glucose utilization was calculated from the time courses of the plasma [^{14}C]deoxyglucose and glucose concentrations and the tissue ^{14}C concentrations by the operational equation of the [^{14}C]deoxyglucose method (*6*).

In another group of animals spreading cortical depression was induced by the application of KCl directly on the surface of the parietal cortex. In these experiments the animal was reanesthetized with intravenous pentobarbital approximately 2 hours after recovery from the halothane–nitrous oxide anesthesia, the exposed dura was opened, and artificial cerebrospinal fluid containing 20 to 80 m*M* KCl was applied to one side of the parietal cortex and artificial CSF without added KCl was applied to the other side. The d-c potential of the cortical surface was monitored continuously by means of Marshall glass pore electrodes (outer diameter, 2 mm) (*2*). The recording electrode was applied to the surface of the cortex approximately 3 mm from the site of KCl application, and the reference electrode was placed in the subcutaneous tissues of the back of the neck. The outputs of the electrodes were amplified in a differential amplifier and displayed on the face of a Tektronix type RM565 oscilloscope or recorded by means of a Beckman model R611 polygraph. Local cerebral glucose utilization was measured under two sets of conditions in these experiments: (i) during sustained spreading cortical depression manifested by repeated waves of negative shifts of d-c potential caused by repeated applications of KCl, and (ii) immediately after return of the d-c potential to the normal value after a single wave of depression