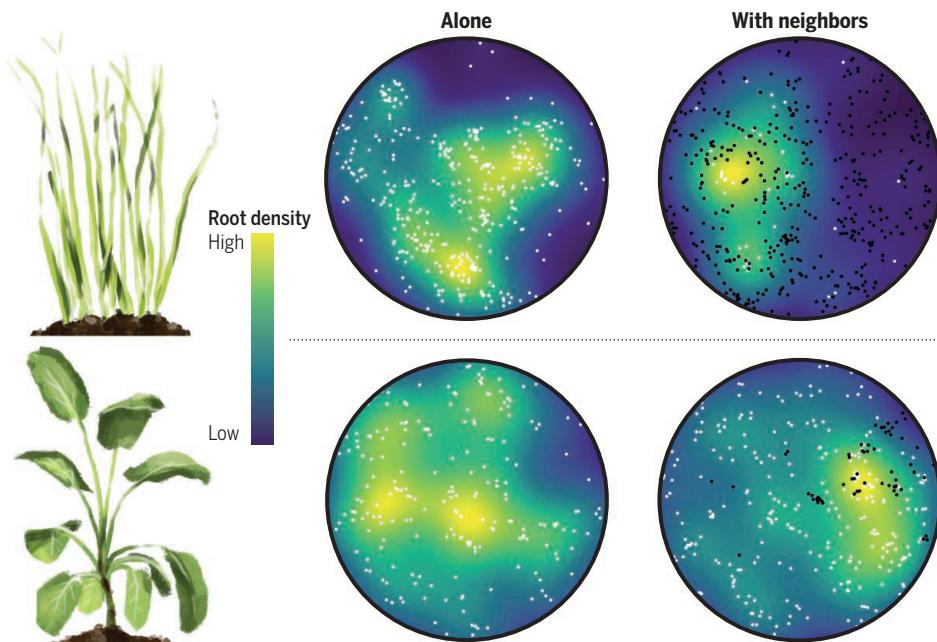


Mapping plant roots

Roots (white dots) explore soil widely in the absence of neighbors (left-hand circles; root density increases from blue to yellow). In the presence of neighbor roots (black dots in the right-hand circles), the plant in the top row keeps roots close to its stem, whereas the plant in the bottom row places them toward neighbors' roots (7). Root mapping enables testing of plant behavioral theory.



varieties with low stature (6) and reduced responsiveness to shading by neighbors (10). Conversely, overproliferation of roots could be enhanced in cover crops to maximize the positive effects on soil organic matter and associated benefits for soil fertility and disease resistance (11).

The dependence of root production on the spatial locations of interacting roots highlights the importance of fine-scale spatial measurements in resolving ongoing debate about plant behavior. By measuring only total root production or root production over large spatial scales, we may miss local over- and underproliferation and risk gathering data that reflect experimental artifacts of soil volume and nutrients (2, 12). However, it should also be recalled that many plant species have evolved in conditions of perpetual competition, seldom growing in the absence of neighbors. Some plants may therefore always overproduce roots close to their stems, independent of neighbor presence. Verifying the existence of selfish overinvestment in root growth would be extremely challenging in such instances. Just as we do not expect trees to stop producing trunks in the absence of surrounding trees, we should not necessarily expect root overproduction to be curtailed in the absence of competition (13).

Current evolutionary models of plant root production do not require that plants are able to detect competitors but are purely driven by resource dynamics, which none-

theless require the existence of complex signaling mechanisms. However, we know that some plant species are capable of detecting the proximity and even genetic identity of neighbors, which may trigger measures to secure resources before direct competition takes place (see the figure) (14). Plants may also assess the relative competitive rank of their neighbors and choose to avoid costly battles with opponents that they have no chance of winning (7, 14). This raises the prospect of greater diversity in plant foraging strategies and points to further avenues for exploration. ■

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NEUROSCIENCE

Stimulating the brain to restore vision

High-definition brain prostheses are developed for treating blindness

By Michael S. Beauchamp and Daniel Yoshor

More than 70 years ago, electrical stimulation of the human visual cortex was shown to elicit the perception of a brief flash of light, or phosphene (1). Subsequently, there were numerous attempts to develop cortical visual prostheses (CVPs) that electrically stimulate the visual cortex to restore vision to people with acquired blindness (2–4). The basic design of a CVP is simple: A head-mounted camera captures the visual scene, and a computer translates it into patterned brain stimulation. However, CVP implementation foundered on technological limitations, especially the size and complexity of the stimulation hardware. Advances in miniaturization and the efficiency of digital circuits suggest that it is time to try again (5, 6). On page 1191 of this issue, Chen *et al.* (7) describe the implantation of more than 1000 electrodes in the visual cortex of nonhuman primates (NHPs) to create artificial vision.

This technical tour de force relied on features of early visual cortex shared by humans and NHPs. The visual cortex takes up a substantial fraction of the cerebral tissue, ~20% in humans. This creates a surface area of many square centimeters that can accommodate the implantation of electrodes. The visual cortex is retinotopic, meaning that there is an orderly mapping between each location in the visual scene and each location in the brain. A CVP with an array of electrodes can provide an array of phosphenes, similar to individual lights comprising a stadium scoreboard, that can be activated to produce visual sensations (percepts).

In natural vision, information from the visual scene moves through a hierarchical network of processing stages, from the retina to the thalamus to primary visual

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cortex (V1) and higher visual areas, such as the fourth visual area (V4). Chen *et al.* implanted electrode arrays in both V1 and V4 of NHPs. For CVPs to function effectively, the current level for each electrode must be individually adjusted so that the current is sufficient to produce a detectable phosphene but not so high that the phosphene expands to cover an extended region of space. This requires time-consuming calibration in which the participant reports their percept at multiple different current levels for every electrode. Chen *et al.* address this problem by stimulating electrodes in V1 while recording from electrodes in V4. They show that it is possible to estimate the appropriate V1 stimulation current from the recorded neuronal responses in V4, a process that could be conducted automatically and rapidly for multiple electrodes.

For millions of patients with damaged or diseased eyes leading to blindness, there are few or no treatment options. Recently,

the stimulation currents are 10- to 100-fold less than that required for electrodes that sit further away atop the cortex, as in the FDA-approved CVP. When hundreds of electrodes are stimulated at once, low currents are essential to minimize both the power consumption of the device and the amount of current injected into the brain.

A number of technological and biological issues remain. On the technological front, the electrode arrays used by Chen *et al.* require a wired connection between the brain and the rest of the CVP. A wireless device will be necessary for long-term implantation of a clinical device in humans. Fortunately, considerable advances in neural stimulation with biocompatible wireless devices mean that solutions are close at hand (8).

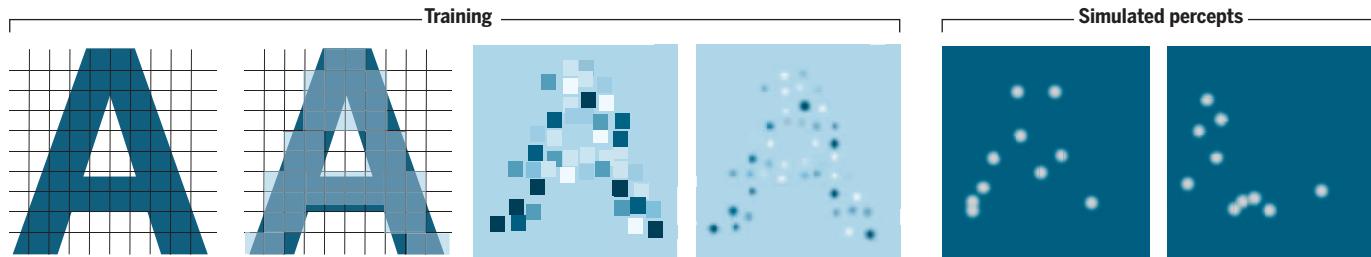
Phosphenes are experienced as bright flashes, not the rich colors and forms that characterize natural vision. The reason for this difference is likely that neurons in V1 respond to simple visual features, such as

lated electrodes to convey information. For instance, the letter T could be conveyed as a horizontal stroke followed by a vertical stroke. Human patients implanted with small numbers of visual cortex electrodes were able to identify letter shapes delivered using a combination of current steering and dynamic stimulation (14).

Future studies should also investigate the full realm of possible transformations between the visual scene and patterned brain stimulation. Advanced machine vision can extract relevant information from the visual scene, which could change based on circumstance. For example, in a navigation task, arrow shapes could be delivered to signal the correct heading direction (15). After decades of false starts, there is a bright future for CVPs. Chen *et al.* set a new benchmark for the next generation of CVPs by demonstrating that 1000 electrodes are sufficient to create percepts of letters, orientation, and motion. Advances in wireless stimula-

Brain stimulation to create artificial vision

Electrical stimulation of the visual cortex is used to create the perception of letters. Letter shapes were decomposed into dot patterns and shown on a computer display to train nonhuman primates (NHPs). The NHPs learned 16 different letters. (An example training pattern for the letter "A" is shown.) Then, between 8 and 15 visual cortex electrodes were stimulated to create artificial percepts. Simulated percepts for the letters "A" (left) and "L" (right) are shown.



six patients were implanted with a CVP in a U.S. Food and Drug Administration (FDA)-approved clinical trial. However, the device has only 60 electrodes, limiting patients to simple tasks such as detecting the light or dark areas in a visual scene. By contrast, the device developed by Chen *et al.* comprises 16 arrays of 64 electrodes each, for a total of 1024 electrodes. The high electrode count meant that Chen *et al.* could arrange phosphenes in the shape of different letters, which the NHPs were trained to discriminate (see the figure). In addition, the NHPs were able to accurately perform simpler tasks, such as making eye movements to the location of a phoshene, determining whether two phosphenes were in a horizontal or vertical configuration, and deciding whether two phosphenes were stimulated in one order or another, creating the impression of apparent motion.

The electrodes used by Chen *et al.* penetrated into the cortex. Because intracortical electrodes are near the stimulated neurons,

oriented lines. Stimulating these neurons produces a correspondingly simple percept (9, 10). Neurons in higher-level visual areas respond to more complex features, and electrical stimulation of these areas can produce the experience of seeing colors (11) or faces (12). It is intriguing to speculate whether the NHPs in the Chen *et al.* study could be induced to see more naturalistic patterns if V4 and V1 were stimulated at the same time.

Even with 1024 electrodes, the letter shapes that can be generated are crude (see the figure). New array technologies with orders-of-magnitude more electrodes will facilitate the generation of more refined shapes. Advanced stimulation algorithms, akin to software that accompanies the CVP hardware, can also be applied. With current steering, electricity is delivered to adjacent electrodes to stimulate tissue between the implanted electrodes, creating more phoshene locations that fill in the retinotopic map (13). Another technique, called dynamic stimulation, uses the sequence of stimu-

tion, high-density electrode fabrication, and stimulation algorithms offer hope that new devices will provide useful visual function for people living with blindness. ■

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