Distant explosion. A pinpoint of light from a type Ia supernova that exploded more than 10 billion years ago is centered in the lower panel. The supernova was revealed by digitally subtracting before and after images of a faint, yellowish, elliptical galaxy that appears in the Hubble Space Telescope Deep Field image shown at the top and left.

burning front is a subsonic nuclear flame. In a delayed detonation model, the deflagration makes a transition to a supersonic detonation. In both models, the velocity of the deflagration is crucial to the outcome, but it has to be treated as an adjustable parameter because the flame is inherently three-dimensional (3D). The density at which the deflagration-detonation transition (DDT) takes place also cannot be calculated in a 1D model.

Gamezo et al. (1) have now calculated a self-consistent 3D deflagration explosion. The total amount of fuel burned, and therefore the kinetic energy and the amount of $^{56}$Ni, are about right to be consistent with observed light curves. The compositional structure, however, is quite unlike those of 1D models that are consistent with observation. Instead of being radially stratified, the elements coexist at all radii. The model spectra are unlikely to be consistent with observations.

The radially mixed compositional structure appears to be an inevitable characteristic of deflagration models, because buoyant burned matter such as $^{56}$Ni and its decay products has time to rise relative to the denser unburned carbon and oxygen. Gamezo et al. (1) conclude that type Ia supernovae must undergo a DDT. Thus, by solving one problem they present another: Calculating DDT will be computationally challenging, especially considering the likelihood that DDT initiates almost simultaneously at various places in the ejected matter (10).

Now that 3D explosion models are beginning to appear, astronomers are gearing up to do 3D radiative transfer calculations so that the spectra of the models can be calculated and compared with observations (11–12). Supernova research is entering a new realm of computational complexity.

**References and Notes**

13. I thank M. Hamuy, R. Lopez, and A. Pastorello for providing the data for the first figure.

**Perspectives: Neuroscience**

To See Is to Attend

Steven Yantis

Neuroscientists who study vision are eager to discover how visual information is encoded in the pattern of neural activity within the more than three dozen visual areas of the brain. Complicating this task is the fact that vision is not a purely stimulus-driven, hard-wired response to visual input. The organism’s state of attention, which depends on goals and expectations, strongly modulates visual responses in the brain (1–4). Indeed, it has been argued persuasively that we experience only that to which we attend (5). Attention is the means by which an organism controls the potentially overwhelming flow of visual input via top-down neural feedback. On page 81 of this issue, Bisley and Goldberg (6) provide new insights into how attentional control of vision is implemented in the primate brain.

Their study investigates neural activity in the lateral intraparietal area (LIP), a subregion of the parietal lobes (see the figure). The parietal cortex, in addition to analyzing visuospatial information and representing plans for limb and eye movements (7), also may be important for controlling the deployment of visual attention (8, 9). For example, responses in LIP and nearby parietal area 7a (see the figure) respond more strongly to stimuli that are salient or behaviorally relevant than to those that are not (10, 11). Functional neuroimaging studies have revealed selective activation of parietal areas during shifts of attention (12–15). However, no clear consensus has emerged about what neurons in the parietal cortex do.

To find out, Bisley and Goldberg trained two monkeys to perform a task that required them to prepare, but not immediately execute, a rapid eye movement or saccade. The monkeys had to plan a saccade from a central “home” location to a remembered location marked by a briefly flashed target dot (see the figure). Then they had to decide whether to make the saccade on the basis of a subsequently flashed probe stimulus. If the probe was a “C” they were to make the saccade, but if it was a mirror-reversed “C” they were to withhold and cancel the saccade. Much previous work has shown that eye movements are preceded by a shift of attention to the new location (saccade goal) (16). In this monkey task, the maintained eye movement plan resulted in an increase in visual sensitivity at the saccade goal that was dependent on attention. The flashed probe could be accurately identified as a normal or mirror-reversed “C” at lower contrast when it appeared at the saccade goal, compared with when it appeared elsewhere. In this way, the monkey was induced to maintain a state of focused attention at the target location while waiting for the probe to appear.

Occasionally, a distractor dot was flashed in a nontarget location. This caused an involuntary, transient shift of attention to the distractor (17), indexed by increased perceptual sensitivity at the distractor location for a few hundred milliseconds after its appearance. The locus of attention then returned to the target location in preparation for the planned saccade. This task thus induced a sequence of

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voluntary and involuntary attention shifts that occurred at well-specified times during the course of each trial of the experiment. Behaviorally, this was reflected in attention-dependent increases in perceptual sensitivity at the target, distractor, and target locations, in turn (see the figure). Bisley and Goldberg recorded the electrical activity of single neurons in the LIP area after mapping the cell’s receptive field (the part of the scene that, when stimulated, drives the cell’s response). They arranged the visual displays in the eye movement task so that either the target or the distractor dot would fall within the currently measured cell’s receptive field.

When the target dot appeared, it evoked a strong transient neuronal response, followed by a sustained, above-baseline discharge that reflected the voluntary deployment of attention to the target location in preparation for the upcoming saccade (see the figure). When the distractor appeared elsewhere, it evoked a transient response in the population of LIP cells with receptive fields in the distractor location (and, importantly, this had no effect on the sustained discharge of the cell monitoring the target location). The response to the distractor returned to baseline within a few hundred milliseconds. Within the brief window of time during which the LIP cells monitoring the distractor location were most active, attention was fixed at that location. As soon as the LIP response in the distractor location fell below that in the target location, attention (as measured behaviorally) shifted back to the target location. For a very brief interval as the response to the distractor was decaying, and during which the responses of these two populations of cells did not differ, behavioral performance was similarly identical. This tight linkage between attention and the responses of LIP cells provides strong evidence that the LIP region of the parietal cortex constitutes a priority map of attention.

These findings offer a possible neural mechanism for an idea that has been advanced in the psychophysical and computational vision literature (18–22). According to these proposals, an attentional priority map continuously represents the importance or salience of every location in the visual field. Spatial attention is deployed to locations in the order of their priority; once visited, the priority at that location is canceled to prevent revisiting recently attended locations (called “inhibition of return”) (23). Changes in the scene or in the observer’s goals are dynamically reflected in the map.

A number of recent studies support a biased-competition model of visual selective attention, indicating a clear role for an attentional priority map (1, 24, 25). Populations of neurons tuned to specific sensory stimuli (for example, a red vertical bar versus a blue horizontal bar) compete for representation: When both stimuli are present in the scene, the response of each neural population is weaker than when either stimulus is presented alone. A top-down feedback signal that reflects the observer’s state of attention is thought to bias the neural competition in favor of the attended object or location. This in turn reinforces the suppression of the unattended object. The attentional priority map may well be a source of the biasing signal.

Many questions remain to be answered. For example, Bisley and Goldberg induced attention shifts that were driven largely by the appearance of stimuli (although the maintenance of attention at the saccade goal required a voluntary intent). It would be of great interest to know whether these LIP cells behave in a similar way to shifts of attention that are purely top-down (for example, in response to an arbitrary auditory cue to attend to the upper right corner of the display).

Another open question is just how these parietal areas of the brain regulate sensory responses in extrastriate areas (for example, V4 and MT) that are known to be strongly modulated by attention (3, 4, 15, 24, 25). Bisley and Goldberg’s observations, together with others that have implicated parietal activity in the control of voluntary shifts of attention (2, 10–15), suggest that parietal outputs may constitute the biasing signal for attention, but the causal link has not yet been definitively established.

Finally, little is known about how voluntary intentions give rise to changes in parietal and occipital areas. Prefrontal cortex—the site of working memory and executive control—is widely believed to be the ult-
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mate source of voluntary attentional control, but this is little more than speculation. Recent findings from monkey neurophysiology and functional brain imaging in humans are providing insights that will move us closer to answering these questions.

References

PERSPECTIVES: ECOLOGY

Social Slime Molds Meet Their Match

Bernard Crespi and Stevan Springer

Alleles of genes that code for altruistic behavior face an identity crisis. Such behaviors are costly, and alleles that cause them can spread only if the benefits of altruism are preferentially directed to individuals that also carry the helpful allele. In most cases, altruistic individuals rise to this challenge probabilistically: They help relatives because their close genetic relationship makes them the best bet for carrying an identical allele. But even relatives are not a sure thing, and the cost of errant helping behavior could be avoided if alleles for altruistic behavior could directly recognize themselves in other individuals. Hamilton (1), in one of his legendary thought experiments, described three conditions that would allow a single gene to direct altruistic benefits toward a copy of itself in another individual. The three conditions are: (i) bearing a phenotype that advertises the allele’s presence (such as a green beard), (ii) recognition of that phenotype in others, and (iii) an altruistic response (that is, preferential treatment) of those recognized. It was Dawkins (2) who coined the colorful metaphor “green beard” to denote such altruistic genes. Biologists had presumed that green-beard genes required too complex an integrated set of effects to have evolved. Their view changed, however, with the discovery of the fire ant gp9 locus (3) and the poison-antidote system of bacteriocin-producing bacteria (4). But these green-beard genes appear to comprise multiple tightly linked loci, so a single gene that could code for character, recognition, and response remained a theoretical curiosity. Enter Queller et al. (5) on page 105 of this issue with their description of single-gene green-beard effects in the slime mold Dictyostelium. Their work provides spectacular confirmation of Hamilton’s musings and demonstrates that social behaviors thought too genetically complex even for altruistic metazoans like ourselves are present in the humblest eukaryotes ever to locomote over damp dirt.

Queller et al.’s finding that social behavior in Dictyostelium is facilitated by green-beard effects has been a long time coming but, as it turns out, is not entirely unexpected. In a feat of inductive logic as remarkable as Hamilton’s initial proposal, Haig (6) described the potential for green-beard genes in maternal-fetal interactions. He even predicted the functional class of protein—a homophilic adhesion protein that binds to itself—that would ultimately yield the first single-gene green beard. Homophilic cell adhesion proteins have exactly the properties required to operate as single-gene green beards. These proteins display themselves conspicuously on the cell surface and function as simple self-recognition systems, that is, they bind to copies of themselves expressed by other cells. Altruistic benefits to other cells can result directly via benefits from aggregation or movement, or indirectly through intimate connections between cell adhesion proteins and intracellular signaling processes (7).

How does simple “find and bind” activity generate multifaceted social effects in slime molds? Dictyostelium exhibits altruistic behavior in its simplest and most extreme form. Starving single cells coalesce into a mass, which transforms into a fruiting body composed of two parts: reproductive spores and nonreproductive stalk cells that altruistically lift the spores high to aid their dispersal to a more food-rich environment (see the figure). Queller et al. recreated in the laboratory an evolutionary struggle for sporulation. They did this by pitting wild-type cells with a functional csA (contact site A) gene, encoding homophilic cell adhesion protein gp80, against knockout cells deficient in csA that showed defective adhesion. Their experiments revealed that wild-type, green-beard cells recognized and pulled one another into and along cooperative streams to form the aggregating mobile slug via binding interactions among the homophilic cell adhesion proteins; but “clean-shaven” knockout cells were left far behind (see the figure). And with good reason—if knockout cells reached the aggregate, their reduced adhesion would displace them toward the trailing edge of the slug, an area that preferentially develops into spores. This would cause the good, green-beard cells to finish last. Such cheating is apparently disfavored, and green-beard alleles resist displacement by less adhesive mutants, just as green beards must have originally spread to supplant them. But might mutations also occur in beard genes encoding other colors, leading to clone-specific and thus nepotistic (rather than promiscuous) cooperation?

The discovery of molecular green beards has implications well beyond the niceties of slime mold social behavior. Single-gene green-beard effects could plausibly alter any biological process involving a close interaction between cells. Homophilic cell adhesion proteins were first studied because of their role in tissue differentiation. Tissue dedifferentiation leading to cancer is associated with expression of an altered suite of cell adhesion proteins, and metastasis correlates with reduced expression of this suite (8). Adhesion proteins whose expression is altered during tumor formation are all ideal green-beard candidates in a naturally selected although pathological context. Interactions between gametes can also be modified by green-beard effects. Cooperative sperm behavior, such as that of paired marsupial sperm (9) or wood mouse