

model of a SN Ia explosion is incomplete. The most natural solution to this problem that would make the results consistent with observations would be to assume that the turbulent flame triggers a detonation. A thermonuclear detonation wave could propagate through the WD with velocities $\sim 10^9$ cm/s (49, 50) and would quickly burn all the material near the center, leaving only the low-density outer layers unburned. For a density below 5×10^7 g/cm³, a detonation would produce intermediate-mass elements (25) that are observed in spectra of SNe Ia. A detonation would also partially smooth out composition inhomogeneities that are predicted by the deflagration model and that may be incompatible with observations (51). Remaining asymmetries may account for a weak polarization recently detected in SN Ia spectra (52, 53).

One-dimensional (25, 28–32) and 2D (26, 27) delayed-detonation models were the most successful in explaining observable characteristics of SNe Ia. These models, however, use the time for detonation initiation as a free parameter because the DDT problem is intrinsically 3D and still unsolved. A large-scale 3D model also cannot reproduce DDT phenomena that involve physical processes occurring on small unresolved scales. One approach to solving this problem is to study in much more detail the types of reacting flows created by 3D deflagrations and to look for situations that create the right types of “hot spots” that we know (54) are the sources of detonation initiation.

References and Notes

- J. C. Wheeler, R. P. Harkness, *Rep. Prog. Phys.* **53**, 1467 (1990).
- A. V. Filippenko, *Annu. Rev. Astron. Astrophys.* **35**, 309 (1997).
- J. C. Wheeler, *Am. J. Phys.*, in press.
- S. E. Woosley, T. A. Weaver, *Annu. Rev. Astron. Astrophys.* **24**, 205 (1986).
- D. Branch, A. M. Khokhlov, *Phys. Rep.* **256**, 53 (1995).
- J. C. Wheeler, R. P. Harkness, A. M. Khokhlov, P. A. Höflich, *Phys. Rep.* **256**, 211 (1995).
- K. Nomoto, K. Iwamoto, N. Kishimoto, *Science* **276**, 1378 (1997).
- D. Branch, *Annu. Rev. Astron. Astrophys.* **36**, 17 (1998).
- W. Hillebrandt, J. C. Niemeyer, *Annu. Rev. Astron. Astrophys.* **38**, 191 (2000).
- A. Burrows, *Nature* **403**, 727 (2000).
- F. Hoyle, W. A. Fowler, *Astrophys. J.* **132**, 565 (1960).
- M. M. Phillips, *Astrophys. J.* **413**, L105 (1993).
- M. Hamuy et al., *Astron. J.* **109**, 1 (1995).
- A. G. Riess, W. H. Press, R. P. Kirshner, *Astrophys. J.* **438**, L17 (1995).
- S. Perlmutter et al., *Nature* **391**, 51 (1998).
- S. Perlmutter et al., *Astrophys. J.* **517**, 565 (1999).
- B. P. Schmidt et al., *Astrophys. J.* **507**, 46 (1998).
- A. G. Riess et al., *Astron. J.* **116**, 1009 (1998).
- A. G. Riess et al., *Astrophys. J.* **560**, 49 (2001).
- P. A. Höflich et al., *Astrophys. J.* **472**, L81 (1996).
- W. D. Arnett, *Astrophys. Space Sci.* **5**, 180 (1969).
- C. J. Hansen, J. C. Wheeler, *Astrophys. Space Sci.* **3**, 464 (1969).
- K. Nomoto, D. Sugimoto, S. Neo, *Astrophys. Space Sci.* **39**, L37 (1976).
- , F.-K. Thielemann, K. Yokoi, *Astrophys. J.* **286**, 644 (1984).
- A. M. Khokhlov, *Astron. Astrophys.* **245**, 114 (1991).
- D. Arnett, E. Livne, *Astrophys. J.* **427**, 315 (1994).
- , *Astrophys. J.* **427**, 330 (1994).
- H. Yamaoka, K. Nomoto, T. Shigeyama, F.-K. Thielemann, *Astrophys. J.* **393**, L55 (1992).
- A. M. Khokhlov, E. Müller, P. A. Höflich, *Astron. Astrophys.* **270**, 223 (1993).
- P. A. Höflich, *Astrophys. J.* **443**, 89 (1995).
- , A. M. Khokhlov, J. C. Wheeler, *Astrophys. J.* **444**, 831 (1995).
- , A. M. Khokhlov, *Astrophys. J.* **457**, 500 (1996).
- A. M. Khokhlov, available online at <http://arxiv.org/abs/astro-ph/0008463>.
- M. Reinecke, W. Hillebrandt, J. C. Niemeyer, *Astron. Astrophys.* **386**, 936 (2002).
- , *Astron. Astrophys.* **391**, 1167 (2002).
- Materials and Methods are available as supporting material on Science Online.
- A. M. Khokhlov, *Astrophys. J.* **449**, 695 (1995).
- , *J. Comput. Phys.* **143**, 519 (1998).
- F. X. Timmes, S. E. Woosley, *Astrophys. J.* **396**, 649 (1992).
- A. M. Khokhlov, E. S. Oran, J. C. Wheeler, *Astrophys. J.* **478**, 678 (1997).
- , *Combust. Flame* **105**, 28 (1996).
- P. A. Höflich, J. Stein, *Astrophys. J.* **568**, 779 (2002).
- E. Livne, *Astrophys. J.* **406**, L17 (1993).
- A. M. Khokhlov, *Astrophys. J.* **424**, L115 (1994).
- D. J. Jeffery et al., *Astrophys. J.* **397**, 304 (1992).
- A. Fisher, D. Branch, P. Nugent, E. Baron, *Astrophys. J.* **481**, L89 (1997).
- P. A. Mazzali, *Mon. Not. R. Astron. Soc.* **321**, 341 (2001).
- R. P. Kirshner et al., *Astrophys. J.* **415**, 589 (1993).
- A. M. Khokhlov, *Mon. Not. R. Astron. Soc.* **239**, 785 (1989).
- V. N. Gamezo, J. C. Wheeler, A. M. Khokhlov, E. S. Oran, *Astrophys. J.* **512**, 827 (1999).
- R. C. Thomas, D. Kasen, D. Branch, E. Baron, *Astrophys. J.* **567**, 1037 (2002).
- L. Wang, J. C. Wheeler, P. A. Höflich, *Astrophys. J.* **476**, L27 (1997).
- D. A. Howell, P. A. Höflich, L. Wang, J. C. Wheeler, *Astrophys. J.* **556**, 302 (2001).
- A. M. Khokhlov, E. S. Oran, *Combust. Flame* **119**, 400 (1999).
- This work was supported in part by the NASA Astrophysics Theory program (NRA-99-01-ATP-130) and by the Naval Research Laboratory through the Office of Naval Research. Computing facilities were provided by the Department of Defense High Performance Computing Modernization Program. We would like to thank D. Branch, P. A. Höflich, E. Livne, M. Reinecke, L. Wang, and J. C. Wheeler for helpful discussions and the referees for useful comments.

Supporting Online Material

www.sciencemag.org/cgi/content/full/1078129/DC1
Materials and Methods
Figs. S1 and S2
Table S1
Movies S1 and S2

5 September 2002; accepted 22 October 2002
Published online 22 November 2002;
10.1126/science.1078129
Include this information when citing this paper.

Neuronal Activity in the Lateral Intraparietal Area and Spatial Attention

James W. Bisley* and Michael E. Goldberg

Although the parietal cortex has been implicated in the neural processes underlying visual attention, the nature of its contribution is not well understood. We tracked attention in the monkey and correlated the activity of neurons in the lateral intraparietal area (LIP) with the monkey's attentional performance. The ensemble activity in LIP across the entire visual field describes the spatial and temporal dynamics of a monkey's attention. Activity subtending a single location in the visual field describes the attentional priority at that area but does not predict that the monkey will actually attend to or make an eye movement to that location.

Visual attention, the ability to select a portion of the visual world for further processing, is necessary for the perception of the world

Laboratory of Sensorimotor Research, National Eye Institute, Bethesda, MD 20892, USA; Department of Neurology, Georgetown University School of Medicine, Washington, DC 20007, USA; Mahoney Center for Mind and Brain, Keck Center for Cognition and Plasticity, Center for Neurobiology and Behavior, Departments of Neurology and Psychiatry, Columbia University College of Physicians and Surgeons, and the New York State Psychiatric Institute, New York, NY 10032, USA.

*To whom correspondence should be addressed at Mahoney Keck Center for Mind and Brain, Center for Neurobiology and Behavior, New York State Psychiatric Institute, Unit 87, Room 5-06, 1051 Riverside Drive, New York, NY 10032, USA. E-mail: jwb2003@columbia.edu

around us (1). A number of studies have suggested that the lateral intraparietal area (LIP) of the posterior parietal cortex is involved in the generation of visual attention (2–6), on the basis of the well-established phenomenon of attentional enhancement of visual responses: A stimulus that is behaviorally important usually evokes an enhanced response relative to when that stimulus is unimportant. The enhanced response has traditionally been interpreted as reflecting attention to the stimulus itself, but some exceptions bring this interpretation into question. For example, in a cued visual reaction time task, the parietal response to a validly cued stimulus is often less than that to an invalidly cued stimulus (3, 7). Furthermore, the probability of perceiving a stimulus at threshold

RESEARCH ARTICLES

depends not on the properties of the stimulus itself but rather on the subject's visual attention when the stimulus appears (8, 9). To understand the relation of parietal activity to attention, we correlated the responses of neurons in LIP of monkeys with performance on a new task designed to measure both

the spatial and temporal aspects of attention.

Measuring attention in the monkey.

Three methods have been used to describe the locus of attention: a post hoc method (10); a reaction time method (11–13); and a contrast sensitivity method, which defines the spatial locus of attention as that area of the visual

field with enhanced visual sensitivity (14–18). We used the latter because it allowed us to examine how attention changed over time and under different visual conditions (19).

Our task (fig. S1) had two components: the monkeys had to plan a saccade (rapid eye movement) to a remembered location and later had to decide whether to make the movement on the basis of a GO/NOGO stimulus (the probe). We varied the contrast of the probe and used each monkey's response to determine its contrast threshold. An animal's performance was better when the probe appeared at the location where the target had appeared (the saccade goal) than when it appeared elsewhere (Fig. 1A). This improved performance at the saccade goal was significant throughout the task [$P < 0.05$ by paired t test (Fig. 1B)]. We suggest that this lowering of the threshold is an index of the attention allocated to the goal of the planned saccade (17, 18, 20, 21), and that the higher thresholds for the probe at other locations (22) represent the monkey's performance at loci to which attention has not been allocated a priori. We believe this difference is due to a true enhancement in sensitivity at the saccade goal and not to an increase in task difficulty caused by the spatial separation of the saccade target and the probe. The latter would have caused an upward rather than the observed leftward shift in the psychometric function (23).

A flashed object (8, 9, 24, 25) or a pop-out stimulus (26) can attract attention, so we introduced a flashed, task-irrelevant distractor during the delay. The distractor was flashed on half of the trials and was presented either at the saccade goal or opposite the saccade goal (fig. S1B). The distractor was identical to the target in size, brightness, and duration, but appeared 500 ms after the target. When the distractor appeared in the opposite location to the target and the probe appeared 200 ms later, the perceptual threshold went down to the attentionally advantaged level at the site of the distractor (Fig. 1, C and D, red points) and rose to the baseline level at the saccade goal (Fig. 1, C and D, blue points). However, 700 ms after the distractor had appeared, performance was once again enhanced at the saccade goal and not at the distractor location, as was the case 1200 ms after the distractor appeared in monkey I, with a trend toward that result in monkey B. Thus, as in humans, a monkey's attention is involuntarily drawn to a flashed distractor. This occurs even when the animal is planning a saccade elsewhere, but the attentional effect of the distractor lasts for less than 700 ms, by which time attention has returned to the saccade goal. An important feature is the consistency of the attended performance. We found that whenever attention is placed at a location, whether driven there by the upcoming saccade (endogenous attention) or by the flashed distractor (exogenous attention), the

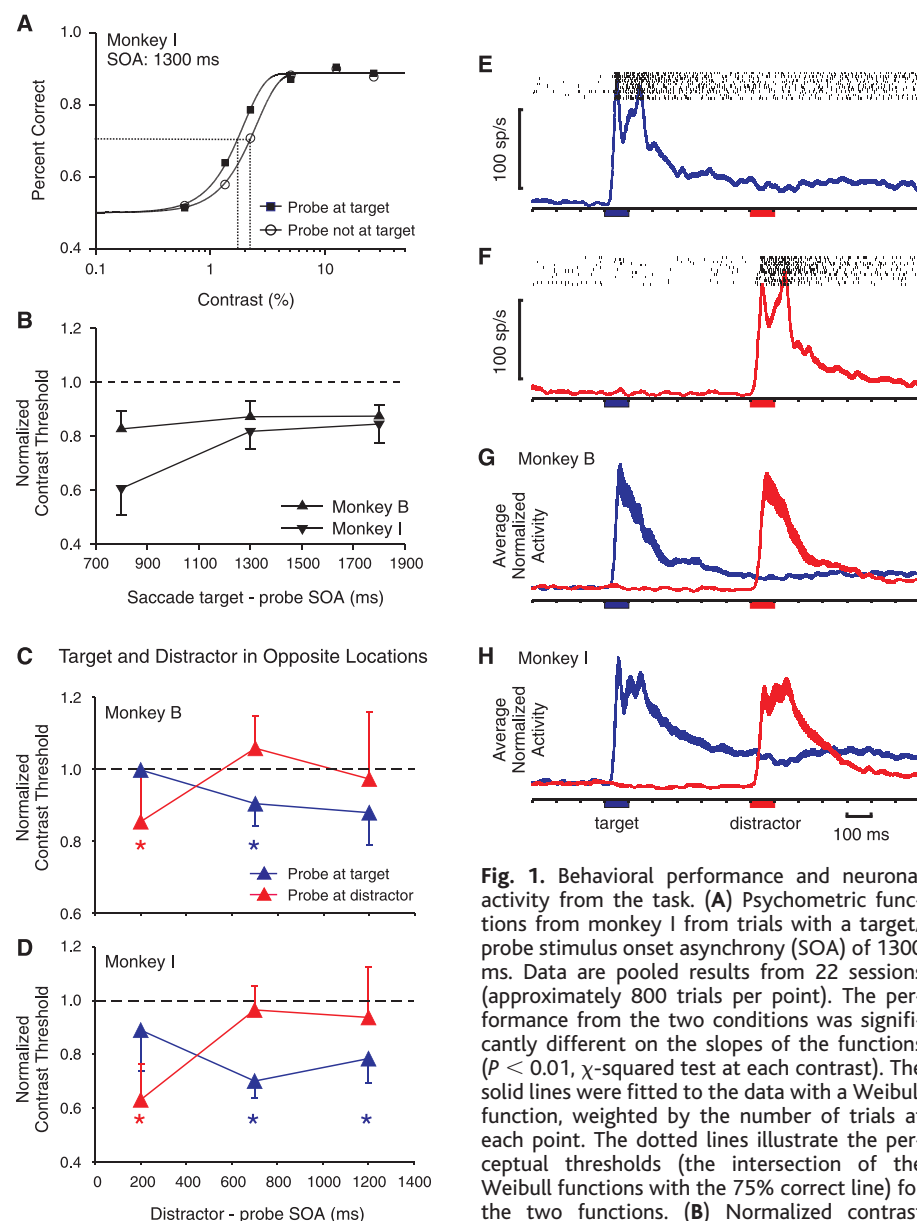


Fig. 1. Behavioral performance and neuronal activity from the task. (A) Psychometric functions from monkey I from trials with a target/probe stimulus onset asynchrony (SOA) of 1300 ms. Data are pooled results from 22 sessions (approximately 800 trials per point). The performance from the two conditions was significantly different on the slopes of the functions ($P < 0.01$, χ -squared test at each contrast). The solid lines were fitted to the data with a Weibull function, weighted by the number of trials at each point. The dotted lines illustrate the perceptual thresholds (the intersection of the Weibull functions with the 75% correct line) for the two functions. (B) Normalized contrast thresholds for the three SOAs from the two monkeys when the probe was at the location of the saccade goal. Data for each delay were normalized by the performance at that delay when the probe was not at the saccade goal (illustrated by the dashed line). Points significantly beneath the dashed line show attentional enhancement, and all points were significantly beneath the line (paired t test on prenormalized data). (C and D) Normalized contrast thresholds from trials in which the distractor appeared away from the saccade goal. Points significantly beneath the dashed line show attentional enhancement (asterisk indicates $P < 0.05$, paired t test on prenormalized data). (E and F) Responses of LIP neurons to the target appearing in the receptive field and the distractor appearing outside of the receptive field (blue traces) and to the distractor appearing in the receptive field after the target had appeared outside of the receptive field (red traces). Trace thickness represents the SEM, and the solid blue and red bars show the time and duration of the target and distractor, respectively. (G and H) Raster plots spike density functions from a single cell in LIP were recorded while the monkey was performing the task on threshold. (G) Averaged normalized spike density functions from 18 cells from monkey B. (H) Averaged normalized spike density functions from 23 cells from monkey I.

attentional advantage produced a similar benefit in performance.

Neuronal responses in LIP during the task. We hypothesized that activity in LIP would correlate with the placement of attention. We recorded the activity of 41 neurons in LIP with peripheral receptive fields in two hemispheres of the two monkeys from whom we gathered the psychophysical data. The neurons all had at least visual activity or both visual and memory activity. Figure 1, E and F, shows the response of a single neuron during the trials in which the target appeared in the receptive field of the neuron while the distractor flashed elsewhere (blue trace) and during the trials in which the distractor was presented in the receptive field and the target elsewhere (red trace). There was no difference between the responses for the saccade plan and the distractor measured at threshold or suprathreshold probe contrasts (supporting online text).

We normalized the responses of all the neurons by the mean value of all the points from each trial type for each cell and then calculated the average normalized activity for each animal (Fig. 1, G and H). These data represent a population response to two different events: (i) the appearance of the target and the subsequent generation of the memory-guided saccade, and (ii) the appearance of the distractor. Although we recorded the response of each of the neurons to those two events, one could as easily reinterpret the activity as that simultaneously seen in two different populations of neurons, one with receptive fields at the saccade goal and the other with receptive fields at the distractor site.

A comparison of the monkeys' performance (Fig. 2, A and B, triangles) with activity in LIP (Fig. 2, A and B, lower plots) reveals a consistent relation between activity in LIP and the region of enhanced sensitivity. At any given time throughout the trial, the attentionally advantaged part of the visual field was that which lay in the receptive fields of LIP population with the highest discharge. There was no direct relationship between the absolute amount of activity at a given site in LIP and the attentional advantage. The attentional advantage appeared to be binary, whereas the activity in LIP was graded.

The appearance of the distractor outside of the receptive field had no significant effect on the delay period activity across the sample as a whole and in all but four cells (fig. S2A). As activity in the distractor population began to wane, there was a small but significant increase in the discharge rate of the target population (fig. S2B). Soon after, the level of activity evoked by the flashed distractor crossed the level of activity in the target population. For each monkey, there was a window of 80 to 90 ms (its time of equal activity or window of ambiguity) in which there was no significant difference between the activity evoked by the

distractor and the activity related to the saccade plan ($P > 0.05$ by Wilcoxon signed-rank test, gray columns in Fig. 2, A and B).

After we determined the time of this win-

dow of ambiguity, we went back and measured the contrast thresholds at the saccade goal and at the distractor site at three different times for each monkey: its time of equal

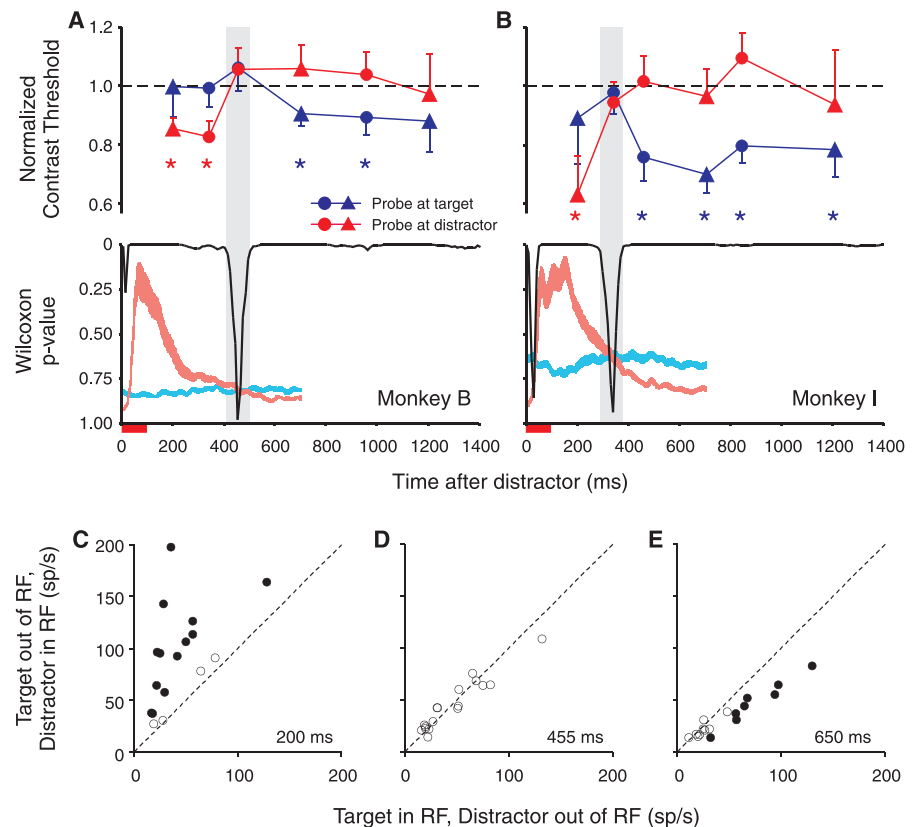
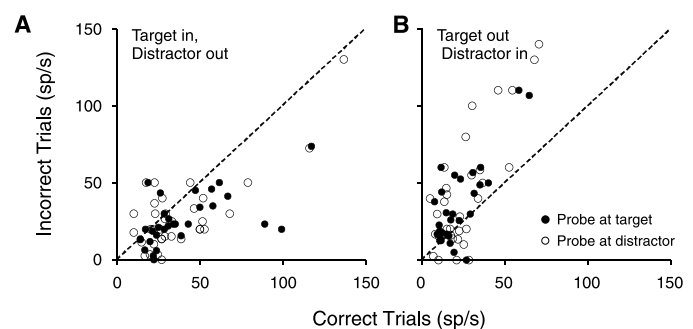


Fig. 2. Comparison of LIP response and monkey behavior. (A and B) Top: Behavioral performance of the monkeys when the probe was placed in the target (blue) or distractor (red) location in trials in which the target and distractor were in opposite locations. Triangles represent data shown in Fig. 1, C and D; circles represent data from psychophysical experiments performed after the single-unit data in Fig. 1, E to H, were recorded. Bottom: Black traces show the P values from Wilcoxon paired signed-rank tests performed on the activity of all the neurons for a monkey over a 100-ms bin, measured every 5 ms. Red and blue traces are taken from Fig. 1, G and H. The vertical gray column signifies the period when there is no statistical difference between the activity in both populations. In each monkey, there was no psychophysical attentional advantage when there was no significant difference in the neuronal response. (C to E) A comparison of the activity when the distractor, but not the target, was in the receptive field (RF) with the activity when the target, but not the distractor, was in the receptive field, from one monkey. These plots represent three of the time periods measured to make the black trace in (A). Solid circles represent cells with significant differences in response (t test, $P < 0.05$). Sp/s, spikes per second. (C) Mean activity 150 to 250 ms after the onset of the distractor for monkey B. (D) Mean activity during a 100-ms epoch centered at the point of equal activity for monkey B (455 ms after the onset of the distractor). (E) Mean activity 600 to 700 ms after the onset of the distractor for monkey B.

Fig. 3. Comparison of activity in correct and incorrect trials 100 ms before the appearance of the probe, plotted separately for probe location. (A) Trials in which the target, but not the distractor, appeared in the receptive field. (B) Trials in which the distractor, but not the target, appeared in the receptive field. Data are shown only for neurons that had errors in both stimulus configurations.



activity and 500 ms later (455 and 955 ms for monkey B and 340 and 840 ms for monkey I) and the other monkey's time of equal activity (Fig. 2, A and B, circles). At the time of equal activity, there was no spatial region of enhanced sensitivity in either monkey, but within 500 ms attention had shifted back to the

site of the target in both monkeys, with normalized thresholds similar to those seen in the earlier experiment. Furthermore, each monkey had the appropriate attentional and neuronal advantages at the other monkey's time of neuronal ambiguity.

Although at times there is only a small dif-

ference in the normalized activity of neurons representing the attentionally advantaged and unadvantaged spatial locations, this difference is extraordinarily robust across the population (Fig. 2, C to E). We included all classes of neurons that we encountered, because the major outputs from LIP are produced by all the classes of neurons found in LIP (27, 28), and we have separately illustrated those with (solid circles) and without (open circles) statistically significant differences in their responses ($P < 0.05$ by t test). Generally, those neurons without significant differences in late-delay activity (Fig. 2E) were those that had no activity during the delay period of the memory-guided saccade task.

There was also a relation between the performance of an animal and activity in its LIP during the 100 ms before the probe appeared in correct and incorrect trials for the two stimulus configurations (Fig. 3). The activity evoked by the saccade plan was lower on error trials than on correct trials, but the activity evoked by the distractor was higher on error trials than on correct trials. This activity did not vary with probe location.

Neuronal responses to the probe. Many previous studies have suggested that an enhanced parietal response to an object reflects attention to that object (2, 29, 30). We found instead that the responses evoked by the probe itself did not correlate with our measure of attention. When the probe was in the receptive field, the initial on-responses were identical whether the cue dictated GO to the receptive field, GO elsewhere, or NOGO (Fig. 4, A and B). After 100 ms, these responses diverged. When the probe signaled GO elsewhere, the response fell rapidly (blue trace). When the probe signaled GO to the receptive field, the response fell more slowly and returned to the pre-probe delay-period level (green trace). When the probe signaled NOGO and the monkey was planning a saccade to the receptive field, the response fell far less rapidly, as if a stimulus requiring a cancellation of the planned saccade evoked attention longer than one confirming it (red trace). Across the sample, the response to this cancellation was significantly greater than the response to the confirmation signal when the saccade plan was to the receptive field (Fig. 4C), and even more so when the saccade plan and its associated attentional advantage were directed away from the receptive field (Fig. 4D). When the response finally fell, however, it fell to the level of the GO-elsewhere response. We found no difference between the response to the GO probe (a Landolt ring) and the response to the complete rings in trials in which the saccade plan was directed to the receptive field (Fig. 4E) or away from it ($P > 0.2$, Wilcoxon paired signed-rank test). Nor was there any difference in the on-responses to the probe in correct and in-

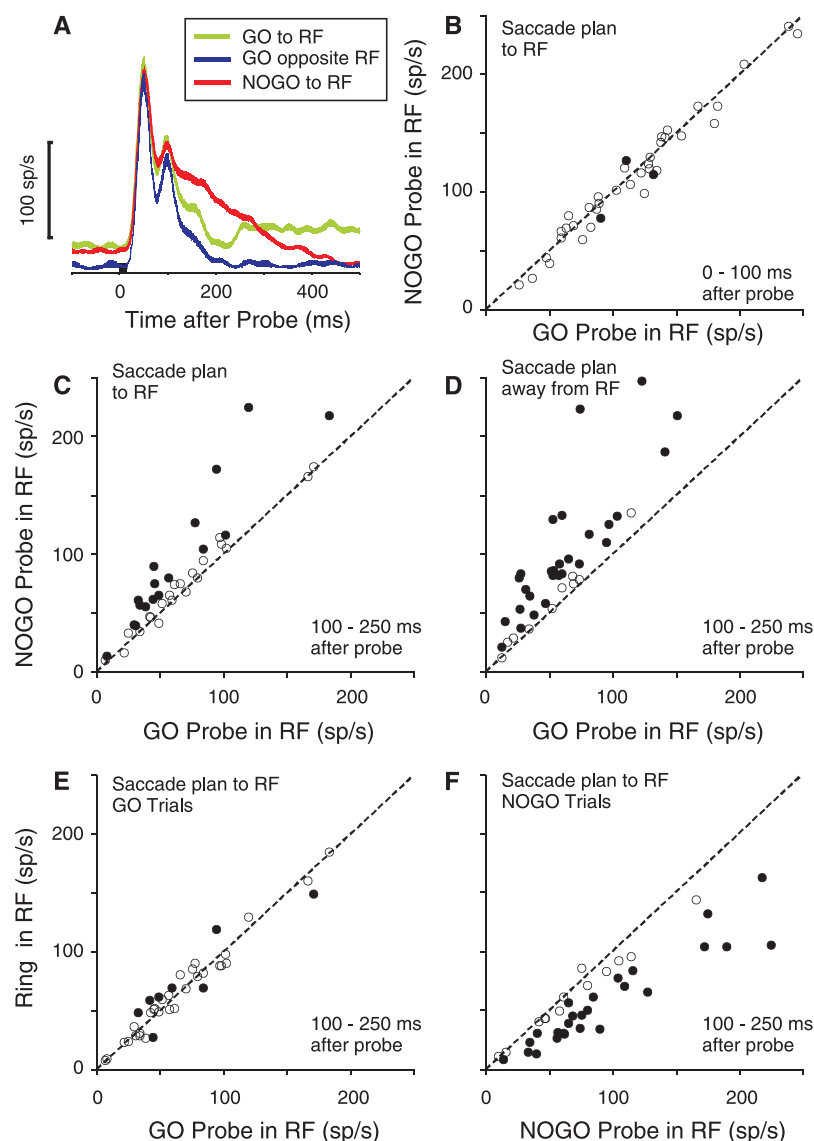


Fig. 4. The response to the probe in the receptive field. (A) Spike density functions from the same neuron illustrated in Fig. 1, E and F. Data are from trials in which the monkey was instructed to plan a saccade into the receptive field, and either the GO stimulus (green trace) or the NOGO stimulus (red trace) appeared in the receptive field, and from trials in which the saccade goal was opposite the receptive field and the GO probe appeared in the receptive field (blue trace). The timing of the stimulus presentation is represented by the black bar starting at 0 ms. (B) The response to the NOGO stimulus plotted against the response to the GO stimulus in trials in which the monkey was instructed to plan a saccade to the receptive field. In (B) to (F), solid circles show data from cells in which the difference in activity was significant ($P < 0.05$, t test); open circles show data from cells in which there was no significant difference. (C) The response to the NOGO stimulus plotted against the response to the GO stimulus in trials in which the monkey was instructed to plan a saccade to the receptive field. (D) The response to the NOGO stimulus plotted against the response to the GO stimulus in trials in which the monkey was instructed to plan a saccade away from the receptive field. (E) The response to the complete ring plotted against the response to the GO stimulus in trials in which the monkey was instructed to plan and execute a saccade to the receptive field. (F) The response to the complete ring plotted against the response to the NOGO stimulus in trials in which the monkey was instructed to plan and then cancel a saccade to the receptive field.

correct trials. However, the enhanced cancellation response was only seen for the actual NOGO probe and not for a ring in the receptive field when the NOGO probe appeared outside of the receptive field (Fig. 4F).

LIP and attention: A new perspective.

Whenever we found an attentional advantage in performance, whether it was driven by the upcoming saccade or by the flashed distractor, the perceptual advantage at the attended location was always the same. However, the activity in LIP was graded. Thus, the attentional advantage lay in the spatial location subtended by the receptive fields of the neurons with the greatest activity, regardless of the absolute value of that activity. For instance, the activity at the saccade goal was sufficient to sustain the attentional advantage until it was swamped by the activity evoked by the distractor. Because of the fall of the visual transient evoked by the distractor, there was a period of about 90 ms, the window of neuronal ambiguity, during which the activity evoked by the saccade plan and distractor did not differ. Although the activity at both locations was above baseline, there was no attentional advantage at either site.

Thus one cannot ascertain a monkey's locus of attention by measuring the activity of a single neuron in LIP, or even by measuring the activity of all the neurons in whose receptive field a given object lies. Instead, one must look at the activity of the ensemble of LIP neurons representing all of the visual field. In this case, we can interpret the graded responses of the discharge at a given site in LIP as providing an attentional priority associated with the object in the subtended receptive field. We found little or no interaction within LIP, suggesting that the attentional priority of each part of the field is predominantly independent. Furthermore, evidence that attention encompasses a region of visual space around the attended stimulus has been found both psychophysically (31) and physiologically (32).

It is unclear what regions of the brain may be involved in the process we have suggested. Other cortical and subcortical areas show modulation of activity that may be related to the allocation of attention, such as the frontal eye field (33, 34) and the superior colliculus (35). Indeed, microstimulation of the frontal eye field has been shown to improve performance in a contrast sensitivity task (16). However, the anatomical projections and graded responses seen in most of these areas suggest that they participate, along with LIP, in a distributed network that drives visual attention. We suggest that it is this distributed network that provides the bias for the biased competition model of attention postulated by Desimone and Duncan (36).

The visual activity of neurons in the posterior parietal cortex is modulated by the salience of the stimulus in their receptive fields (4, 29).

Such enhanced responses have been considered to reflect the attention to the object that evokes the response (2, 10); however, a few studies have called this concept into question. For instance, the intensity of responses in the ventral intraparietal and middle temporal areas did not correlate with the attention paid to the stimuli (30); in a cued visual attention task, the activity evoked by a validly cued stimulus was less than that evoked by an invalidly cued one, even though attention lay at the site of the validly cued stimulus (3). It has been suggested that LIP is more important in determining a shift of visual attention to a stimulus than in maintaining attention to it (3, 37). Our results show that the activity in LIP does, in fact, continuously describe the locus of attention but that this cannot be determined by looking at only one neuron or the representation in LIP of one spatial location. Although LIP does describe the locus of attention, the activity evoked by a stimulus does not necessarily define the attention to that stimulus. We postulate that the enhanced response evoked by an attended stimulus serves to reinforce the attentional priority of its locus rather than providing an original attentional selection.

The locus of attention is defined by a leftward shift in a psychophysical curve and not by performance on a trial-by-trial basis. However, activity in LIP did predict monkey behavior in one sense: When a monkey performed the task correctly, responses to the distractor measured in the 100 ms before the probe appeared were less than when the monkey failed to perform the task correctly, even on those trials in which the probe appeared at the distractor site. Conversely, activity at the saccade goal was greater on correct trials, even when the NOGO probe appeared at the saccade goal. We suggest that this activity in LIP provides a general index of the quality of a monkey's performance: When a monkey was doing its job efficiently, activity at the saccade goal was greater and the response to the distractor was weaker. Thus, the ratio of the activity at the saccade goal and at the distractor predicts the efficiency of a monkey's performance, regardless of the actual geometry of the task.

Attention and motor intention. A number of studies have suggested that LIP is a part of the system for planning saccadic eye movements, on the basis of its activity in the delayed saccade task (38–43). The strongest evidence for this is that delay-period activity of LIP neurons is greater when the neurons describe the target of a saccade than when they describe the target of a simultaneously generated arm movement to a different location (38–39). In light of our current findings, we would interpret these data as predicting that the saccade goal should have a higher attentional priority than the reach goal (17, 21). Furthermore, our results render the motor intention interpretation unlikely for a

number of reasons. The first is that visual attention is pinned to the spatial location of a saccade goal for the duration of the delay period in a memory-guided saccade task; therefore, one cannot distinguish a priori whether LIP activity during the delay period is related to attention or to a motor plan. The second is that when there is a separation between the locus of attention and the saccade goal, the ensemble of neurons in LIP accurately predicts the locus of attention even when there is a conflict between the motor plan and the current locus of attention. Conversely, LIP activity does not predict where, when, or even if a saccade will occur (5, 6). Because attention is ordinarily pinned at the goal of a saccade, it is not unreasonable for LIP to have a faithful replica of a saccade plan. However, because of the many other attention-worthy events that also drive LIP, the saccade plan can be contaminated in a way that renders it useless as a motor signal. In fact, concurrent recordings of local field potentials (which represent synaptic input to LIP) and single-unit recordings have shown that the inputs to LIP contain far more information about an upcoming saccade than the spiking outputs do (44). The third and most dramatic reason is the activity in LIP evoked by the NOGO signal at the saccade goal. This activity is greater than that evoked by the GO signal at the same site. It is difficult to argue that a motor intention signal increases for several hundred ms in response to a signal canceling the intended movement and responds less to a signal confirming it. It is far easier to argue that one attends more to a signal requiring a change of plan than to a signal that confirms the plan.

Of course, LIP has a strong projection to the oculomotor system, with monosynaptic projections to and from the frontal eye field and monosynaptic projections to and disynaptic projections from the superior colliculus (45). Generally, there is a strong correlation between attended objects and saccade targets in the visual field (18, 46). However, this correlation is not obligate, and our results show that in the very circumstances where there is dissonance between a saccade plan and LIP activity, the oculomotor system must ignore LIP. In contrast, we are unaware of any exception to the correlation between the ensemble of activity in LIP and the attentionally advantaged spatial location.

References and Notes

1. R. A. Rensink, *Vision Res.* **40**, 1469 (2000).
2. C. L. Colby, J. R. Duhamel, M. E. Goldberg, *J. Neurophysiol.* **76**, 2841 (1996).
3. D. L. Robinson, E. M. Bowman, C. Kertzman, *J. Neurophysiol.* **74**, 698 (1995).
4. J. P. Gottlieb, M. Kusunoki, M. E. Goldberg, *Nature* **391**, 481 (1998).
5. J. Gottlieb, M. E. Goldberg, *Nature Neurosci.* **2**, 906 (1999).

6. K. D. Powell, M. E. Goldberg, *J. Neurophysiol.* **84**, 301 (2000).
7. M. A. Steinmetz, C. E. Connor, C. Constantinidis, J. R. McLaughlin, *J. Neurophysiol.* **72**, 1020 (1994).
8. S. Yantis, J. Jonides, *J. Exp. Psychol. Hum. Percept. Perform.* **10**, 601 (1984).
9. H. E. Egeth, S. Yantis, *Annu. Rev. Psychol.* **48**, 269 (1997).
10. M. E. Goldberg, R. H. Wurtz, *J. Neurophysiol.* **35**, 560 (1972).
11. M. I. Posner, Q. J. Exp. Psychol. **32**, 3 (1980).
12. E. M. Bowman, V. J. Brown, C. Kertzman, U. Schwarz, D. L. Robinson, *J. Neurophysiol.* **70**, 431 (1993).
13. E. A. Witte, M. Villareal, R. T. Marrocco, *Behav. Brain Res.* **82**, 103 (1996).
14. H. S. Bashinski, V. R. Bacharach, *Percept. Psychophys.* **28**, 241 (1980).
15. V. M. Ciaramitaro, E. L. Cameron, P. W. Glimcher, *Vision Res.* **41**, 57 (2001).
16. T. Moore, M. Fallah, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 1273 (2001).
17. E. Kowler, E. Anderson, B. Doshier, E. Blaser, *Vision Res.* **35**, 1897 (1995).
18. H. Deubel, W. X. Schneider, *Vision Res.* **36**, 1827 (1996).
19. Materials and methods are available as supporting material on Science Online.
20. M. Shepherd, J. M. Findlay, R. J. Hockey, Q. J. Exp. Psychol. A **38**, 475 (1986).
21. J. E. Hoffman, B. Subramaniam, *Percept. Psychophys.* **57**, 787 (1995).
22. The mean normalized thresholds (\pm SEM) for the three nontarget locations were 1.03 ± 0.05 , 1.02 ± 0.06 , and 0.95 ± 0.03 for monkey B and 1.01 ± 0.08 , 1.04 ± 0.08 , and 0.95 ± 0.06 for monkey I.
23. The mean asymptotic performances (\pm SEM) at and away from the saccade goal were $90.7 \pm 1.2\%$ and $90.0 \pm 1.2\%$ for monkey I and $94.2 \pm 0.7\%$ and $93.0 \pm 0.7\%$ for monkey B. The mean slopes (\pm SEM) at and away from the saccade goal were 2.37 ± 0.43 and 2.34 ± 0.32 for monkey I and 2.22 ± 0.34 and 2.59 ± 0.28 for monkey B.
24. K. Nakayama, M. Mackeben, *Vision Res.* **29**, 1631 (1989).
25. S. Yantis, J. Jonides, *J. Exp. Psychol. Hum. Percept. Perform.* **22**, 1505 (1996).
26. J. S. Joseph, L. M. Optican, *Percept. Psychophys.* **58**, 651 (1996).
27. M. Pare, R. H. Wurtz, *J. Neurophysiol.* **85**, 2545 (2001).
28. S. Ferraina, M. Pare, R. H. Wurtz, *J. Neurophysiol.* **87**, 845 (2002).
29. M. C. Bushnell, M. E. Goldberg, D. L. Robinson, *J. Neurophysiol.* **46**, 755 (1981).
30. E. P. Cook, J. H. Maunsell, *J. Neurosci.* **22**, 1994 (2002).
31. D. LaBerge, R. L. Carlson, J. K. Williams, B. G. Bunney, *J. Exp. Psychol. Hum. Percept. Perform.* **23**, 1380 (1997).
32. C. E. Connor, D. C. Preddie, J. L. Gallant, D. C. Van Essen, *J. Neurosci.* **17**, 3201 (1997).
33. A. Murthy, K. G. Thompson, J. D. Schall, *J. Neurophysiol.* **86**, 2634 (2001).
34. T. Sato, A. Murthy, K. G. Thompson, J. D. Schall, *Neuron* **30**, 583 (2001).
35. M. A. Basso, R. H. Wurtz, *J. Neurosci.* **18**, 7519 (1998).
36. R. Desimone, J. Duncan, *Annu. Rev. Neurosci.* **18**, 193 (1995).
37. S. Yantis et al., *Nature Neurosci.* **5**, 995 (2002).
38. L. H. Snyder, A. P. Batista, R. A. Andersen, *Nature* **386**, 167 (1997).
39. L. H. Snyder, A. P. Batista, R. A. Andersen, *J. Neurophysiol.* **79**, 2814 (1998).
40. M. L. Platt, P. W. Glimcher, *J. Neurophysiol.* **78**, 157 (1997).
41. P. Mazzoni, R. M. Bracewell, S. Barash, R. A. Andersen, *J. Neurophysiol.* **76**, 1439 (1996).
42. R. M. Bracewell, P. Mazzoni, S. Barash, R. A. Andersen, *J. Neurophysiol.* **76**, 1457 (1996).
43. R. A. Andersen, C. A. Buneo, *Annu. Rev. Neurosci.* **25**, 189 (2002).
44. B. Pesaran, J. S. Pezaris, M. Sahani, P. P. Mitra, R. A. Andersen, *Nature Neurosci.* **5**, 805 (2002).
45. R. A. Andersen, C. Asanuma, G. Essick, R. M. Siegel, *J. Comp. Neurol.* **296**, 65 (1990).
46. A. L. Yarbus, *Eye Movements and Vision* (Plenum, New York, 1967).
47. We are grateful to the staff of the Laboratory of Sensorimotor Research for assistance in all aspects of this study: J. Raber and G. Tansey for veterinary care; N. Nichols and T. Ruffner for machining; J. McClurkin for help with graphics programming; L. Jensen for electronics; A. Hays for systems programming; C. Rishell and M. Szarowicz for animal care; R. Desimone for comments on a previous version of the manuscript; and M. Smith, J. Steinberg, and B. Harvey for facilitating everything. Supported by the National Eye Institute, the W. M. Keck Foundation, and the Human Frontiers Science Program.

Supporting Online Material

www.sciencemag.org/cgi/content/full/299/5603/81/DC1

Materials and Methods

Supporting Text

Figs. S1 and S2

References and Notes

15 August 2002; accepted 23 October 2002

REPORTS

Dependence of Upper Critical Field and Pairing Strength on Doping in Cuprates

Yayu Wang,¹ S. Ono,² Y. Onose,³ G. Gu,⁴ Yoichi Ando,² Y. Tokura,^{3,5} S. Uchida,⁶ N. P. Ong^{1*}

We have determined the upper critical field H_{c2} as a function of hole concentration in bismuth-based cuprates by measuring the voltage induced by vortex flow in a driving temperature gradient (the Nernst effect), in magnetic fields up to 45 tesla. We found that H_{c2} decreased steeply as doping increased, in both single and bilayer cuprates. This relationship implies that the Cooper pairing potential displays a trend opposite to that of the superfluid density versus doping. The coherence length of the pairs ξ_0 closely tracks the gap measured by photoemission. We discuss implications for understanding the doping dependence of the critical temperature T_{co} .

The superconducting state in a metal is completely suppressed if a sufficiently strong magnetic field is applied. In individual type-II superconductors, the field required—defined as the upper critical field H_{c2} —is an important parameter because it determines the value of the coherence length ξ_0 (the size of the Cooper pair) as well as the strength of the pairing potential; the higher the field H_{c2} ,

the stronger is the pairing potential and the smaller the pair size (l). In the phase diagram of the cuprates, superconductivity has been observed in the range of hole concentration $0.05 < x < 0.25$. Many parameters of the superconducting state, notably the superfluid density and superconducting gap, have been measured as a function of x . The conspicuous exception is H_{c2} , which is uncertain for rea-

sons discussed below. Because even the basic trend of H_{c2} versus x is unknown, the crucial question of whether the pairing strength, as distinct from the superfluid density, increases or decreases with x remains unanswered. We report measurements of H_{c2} versus x in the Bi-based cuprates using the vortex-Nernst effect. In both single and bilayer systems, it was found that H_{c2} (and hence the pairing potential) steeply decreased as x increased. We show that ξ_0 is intimately related to the gap measured by angle-resolved photoemission spectroscopy (ARPES) (2) and results from scanning tunneling microscopy (STM) (3, 4).

In the Nernst effect (5–11), vortices in the vortex liquid state are driven down an applied temperature gradient $-\nabla T \parallel x$. Their velocity v

¹Department of Physics, Princeton University, Princeton, NJ 08544, USA. ²Central Research Institute of Electric Power Industry, Komae, Tokyo 201–8511, Japan. ³Spin Superstructure Project, Japan Science and Technology, Tsukuba 305–8562, Japan. ⁴Physics Department, Brookhaven National Laboratory, Upton, NY 11973, USA. ⁵Department of Applied Physics, ⁶School of Frontier Sciences, University of Tokyo, Tokyo 113–8656, Japan.

*To whom correspondence should be addressed. E-mail: npo@princeton.edu

This copy is for your personal, non-commercial use only.

If you wish to distribute this article to others, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

Permission to republish or repurpose articles or portions of articles can be obtained by following the guidelines [here](#).

The following resources related to this article are available online at www.sciencemag.org (this information is current as of June 5, 2015):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/299/5603/81.full.html>

Supporting Online Material can be found at:

<http://www.sciencemag.org/content/suppl/2003/01/02/299.5603.81.DC1.html>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/content/299/5603/81.full.html#related>

This article **cites 42 articles**, 17 of which can be accessed free:

<http://www.sciencemag.org/content/299/5603/81.full.html#ref-list-1>

This article has been **cited by** 270 article(s) on the ISI Web of Science

This article has been **cited by** 100 articles hosted by HighWire Press; see:

<http://www.sciencemag.org/content/299/5603/81.full.html#related-urls>

This article appears in the following **subject collections**:

Neuroscience

<http://www.sciencemag.org/cgi/collection/neuroscience>