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10 September 1991; accepted 25 November 1991

The Updating of the Representation of Visual Space in Parietal Cortex by Intended Eye Movements

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Every eye movement produces a shift in the visual image on the retina. The receptive field, or retinal response area, of an individual visual neuron moves with the eyes so that after an eye movement it covers a new portion of visual space. For some parietal neurons, the location of the receptive field is shown to shift transiently before an eye movement. In addition, nearly all parietal neurons respond when an eye movement brings the site of a previously flashed stimulus into the receptive field. Parietal cortex both anticipates the retinal consequences of eye movements and updates the retinal coordinates of remembered stimuli to generate a continuously accurate representation of visual space.

AS WE MOVE OUR EYES, A STATIONary object excites successive locations on the retina. Despite this constantly shifting input, we perceive a stable visual world. This perception is presumably based on an internal representation derived from both visual and nonvisual information. Helmholtz proposed that the brain uses information about intended movement to interpret retinal displacements (*1*). We show that single neurons in monkey parietal cortex use information about intended eye movements to update the representation of visual space (*2*).

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The shift in the visual image on the retina produced by a saccade is determined by the size and direction of the eye movement. This predictability enables the representation of visual space in parietal cortex to be remapped in advance of the eye movement. At the single cell level, the intention to move the eyes evokes a transient shift in the retinal location at which a stimulus can excite the neuron.

Our results are summarized schematically in Fig. 1, in which an observer transfers fixation from the mountain top to the tree. During fixation, the representation of the visual scene in parietal cortex is stable. A given neuron encodes the stimulus at a certain retinal location (the cloud). Immediately before and during the saccade, the cortical representation shifts into the coordinates of the next intended fixation. The neuron now responds to the stimulus at a new retinal location (the sun) and stops responding to the stimulus at the initial location (the cloud). The neuron thus anticipates the retinal consequences of the intended eye movement: the cortical representation shifts first, and then the eye catches up. After the eye movement, the representation in parietal cortex matches the reafferent visual input and the neuron continues to respond to the stimulus (the sun). This process constitutes a remapping of the stimulus from the coordinates of the initial fixation to those of the intended fixation.

We demonstrated this remapping by studying the visual responsiveness of neurons in the lateral intraparietal area (LIP) of alert monkeys performing fixation and saccade tasks (*3*). Neurons in LIP have retinocentric receptive fields and carry visual and visual memory signals (*4*). An example is shown in Fig. 2. When the monkey fixates, this neuron responds to the onset of a visual stimulus in its receptive field at a latency of 70 ms (Fig. 2A). Receptive field borders were defined while the monkey maintained fixation, and, under these conditions, stimuli presented outside these borders never activated the neuron. In the saccade task, the fixation target jumps at the same time that a visual stimulus appears. The visual stimulus is positioned so that it will be in the receptive field when the monkey has completed the saccade. If there were no predictive remapping, the cell would be expected to begin discharging 70 ms after the eye movement brings the stimulus into

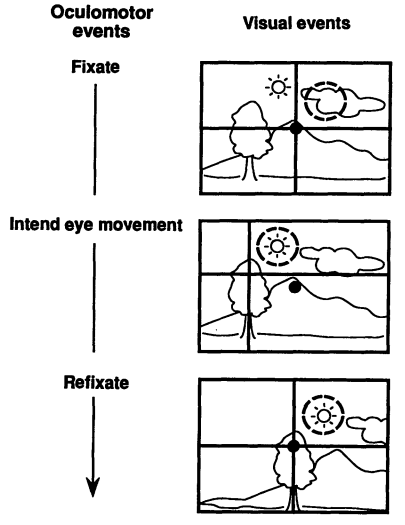

Fig. 1. Remapping of the visual representation in parietal cortex. Each panel represents the visual image at a point in time relative to a sequence of oculomotor events. Receptive field of a parietal neuron, dashed circle; center of current gaze location, solid circle; and coordinates of the cortical representation, cross hairs.

the receptive field. Instead, the cell begins to discharge 150 ms earlier, that is, 80 ms before the beginning of the saccade (Fig. 2B). This early response shows that the location of the receptive field shifted before the eye movement. Completion of the saccade restores the receptive field to its original retinal location, enabling the cell to continue responding to the stimulus as reafferent visual information becomes available.

Remapping is dependent on both the presence of the visual stimulus and the execution of the saccade. The cell discharges neither when the monkey makes a saccade to the target in the absence of the visual stimulus nor when the stimulus is presented at the new location but the monkey does not make the saccade. The cell also does not discharge when the monkey shifts its attention to the saccade target without actually making an eye movement (*5*). Only when the monkey intends to make a saccade that will bring the stimulus into its fixation receptive field does the cell respond. These results indicate that neurons have access not only to visual information in the fixation receptive field but also to information at other retinal locations and to a signal corollary to the saccade. We found that 16 of 36 (44%) of the neurons studied in LIP showed evidence for predictive remapping (*6*).

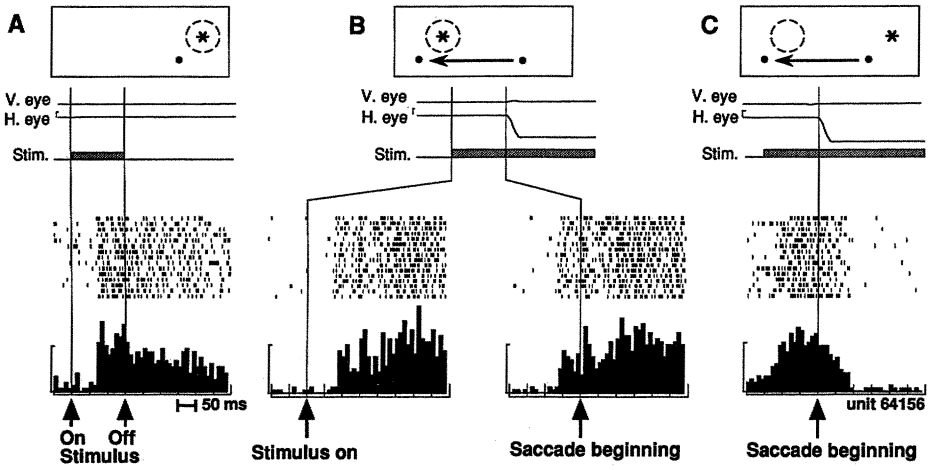

Fig. 2. Effect of impending saccade on visual responsiveness. Diagrams for each condition show the fixation point (dot), visual stimulus (star), receptive field (dashed circle), and saccade (arrow). Time lines below show the horizontal (H.) and vertical (V.) eye position and the beginning and ending of stimulus (Stim.). Raster display shows neuronal responses for 16 consecutive trials. Rasters and histogram are aligned on the event indicated by the long vertical line. Calibration mark at left indicates 100 spikes per second. (**A**) Visual response to stimulus in receptive field in fixation task. (**B**) Visual response to a stimulus that is initially outside of the receptive field. The visual stimulus and the new fixation target appear simultaneously. Left raster aligned on stimulus appearance, right raster on beginning of saccade. Discharge precedes saccade. (**C**) Response after a saccade that removes stimulus from receptive field. Raster aligned on beginning of saccade. Note the truncation of response relative to the response to the disappearance of the stimulus in (A).

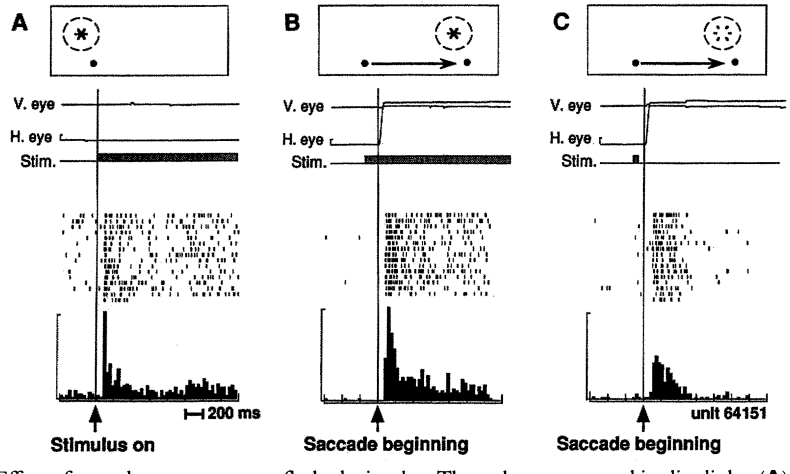

Fig. 3. Effect of saccade on response to flashed stimulus. The task was executed in dim light. (**A**) Visual response to constant stimulus in receptive field. (**B**) Response after saccade that brings stimulus into receptive field. Raster and histogram aligned on beginning of saccade. Response begins when stimulus enters the receptive field. (**C**) Response after saccade when stimulus was flashed for 50 ms. Stimulus is gone before stimulated site enters receptive field.

We also see the effects of remapping when a saccade shifts a stimulus out of the receptive field. The truncation of the visual response is sharper and occurs earlier than would be expected from the response of the neuron when the stimulus is simply extinguished. In the fixation task, the cell gave a tonic visual response that persisted for several hundred milliseconds after the stimulus in the receptive field was extinguished (Fig. 2A). This tonic response was truncated by an eye movement (Fig. 2C), even though the retinal effect was the same as turning off the stimulus.

The above two findings show that some parietal neurons anticipate the retinal consequences of intended eye movements. A third finding reveals that parietal neurons take eye movements into account in their processing of remembered stimuli. Nearly all LIP neurons (22 of 23, 96%) discharge when a saccade brings the site of a flashed stimulus into the receptive field, even though the stimulus itself is no longer present. An example is shown in Fig. 3. This neuron discharged at the onset of a stimulus in the receptive field (Fig. 3A). In the task where a saccade brings the stimulus into the receptive field, this neuron began to discharge only after the saccade (Fig. 3B), thus yielding no evidence for predictive remapping. In the flashed stimulus task, the stimulus is illuminated for 50 ms and is turned off at least 150 ms before the saccade (Fig. 3C). The cell fires after the saccade has brought the location of the stimulus into the receptive field, even though the stimulus is gone. We interpret this discharge as the response to a visual memory trace that has been remapped in conjunction with the eye movement. Control experiments demonstrate that the neuron did not respond to the stimulus in the absence of the eye movement, nor did it respond in relation to the saccade in the absence of the stimulus. The amplitude of the memory trace response averaged about half of that to a stimulus presented in the receptive field. Memory trace responses could be elicited by stimulus flashes less than 50 ms in duration presented even 1 s before the saccade. This finding indicates that the visual memory trace is coded in a retinotopic format that is updated with each eye movement. The remapping of the visual representation in cortex allows visual input from successive fixations to be kept in register.

These results suggest a mechanism for spatial processing of visual information. At the time a saccade is planned, the parietal

representation of the visual world undergoes a shift analogous to the shift of the image on the retina. Unlike the retinal shift that follows an eye movement, the parietal shift precedes the eye movement and predicts the location of reafferent visual input. This dynamic link between successive retinal images may contribute to the integration of visual information across eye movements and to the construction of a continuously accurate, retinocentric representation of visual space.

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6. A neuron without predictive remapping begins to discharge with a visual latency from the time the stimulus enters the receptive field, that is, at the end of the saccade. Any neuron discharging with a shorter latency shows predictive remapping. Because we cannot determine precisely when the stimulus crosses the outer boundary of the receptive field, we adopted a conservative statistical criterion. For each neuron, a *t* test was used to compare mean response latencies for blocks of 16 saccade and fixation trials. Neurons with a latency relative to the beginning of a saccade (when the stimulus is still outside the receptive field) that was shorter or not significantly different from the latency relative to the onset of a stimulus in the fixation task were considered to show predictive remapping.

7. We are grateful to the staff of the Laboratory of Sensorimotor Research for its help: J. Raber for veterinary care, K. Powell and H. Macgruder for animal care, C. Crist and T. Ruffner for machining, L. Jensen for electronics, A. Hayes for computer systems, and J. Steinberg for facilitating everything.

14 June 1991; accepted 10 October 1991

Technical Comment

Enumerating Buckminsterfullerane Isomers

M. Saunders states (*1*) that the number of di-inside isomers of fully reduced $C_{60}H_{60}$ (buckminsterfullerane) is 21, a result that he obtained with the aid of a computer program. He indicates that this number can also be obtained by direct inspection. We carried out such an inspection, using a soccer ball to facilitate the enumeration, and found the number of such isomers to be 23. This number agrees with the result of a computer calculation [using a program written by one of us (G.T.)] and also with the theory of H. G. Pólya (*2*).

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11 September 1991; accepted 16 October 1991

Response: I have reexamined the question of how many di-inside isomers exist for buckminsterfullerane, and I agree that there are indeed 23. However, the main conclusions of my paper are unaffected. Originally, I refined the structure of the symmetric, all-outside, $C_{60}H_{60}$ structure with the molecular mechanics computer program MM3 (*1*). I then obtained the 1770 distances between pairs of carbons and sorted them. The distances appeared to fall into 21 classes. I have now refined the structure further through additional cycles and have made another sorted list of distances. I had previously put the longest 120 distances into a single group (category 21), but the new data show breaks in distance in this group that are quite distinct. Category 21 (60 distances) now has values between 7.48620 and 7.48648 Å. The new category 22 (30 distances) has values between 7.48842 and 7.48874 Å (there is a small break, but it is quite clear). The final category, 23 (30 distances), has values between 7.64422 and 7.64452 Å. (This break between category 22 and category 23 is much larger than that between category 21 and category 22, and I must have overlooked it before.) Additional refinement would make the spread in distances within each category still smaller and the breaks more distinct. Thus, my method does indeed work for this case, but I did not execute it carefully enough originally.

One certainly could make similar kinds of errors with group theory or any other method. However, with sufficient care it should always be possible to get the correct answer with this method. To double-check one's answer, one could separately optimize with MM2 or with any other force field that provides slightly different distances. This would further reduce the odds of a coincidence in distances. The advantage of this new technique is its simplicity; the program for finding and sorting pairs of distances was quickly written and used.

The main point of my paper was that putting hydrogens on the inside of the molecule should greatly lower its energy. This conclusion is unchanged. I have rerun the search program (modified to include the 23 categories of di-inside isomers). Several additional 11-inside isomers were found that were lower in energy than those discovered previously. (In my paper I stated that it was likely that more isomers would be found. This result may have nothing to do with there being 23 classes rather than 21.) None of the new 11-inside isomers are as low in energy as the best 10-inside isomer found so far.

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25 September 1991; accepted 16 October 1991

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