Neural Mechanisms of Saccadic Suppression

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In normal vision our gaze leaps from detail to detail, resulting in rapid image motion across the retina. Yet we are unaware of such motion, a phenomenon known as saccadic suppression. We recorded neural activity in the middle temporal and middle superior temporal cortical areas during saccades and identical image motion under passive viewing conditions. Some neurons were selectively silenced during saccadic image motion, but responded well to identical external image motion. In addition, a subpopulation of neurons reversed their preferred direction of motion during saccades. Consequently, oppositely directed motion signals annul one another, and motion percepts are suppressed.

During and after rapid shifts of gaze we are usually unaware of any image motion or image displacement. Comparable external image motion does not go unnoticed—on the contrary, it has a startling effect. This phenomenon, known as saccadic suppression (*1*), has been extensively investigated psychophysically, but the underlying neuronal mechanisms remain elusive. Some scientists have suggested that vision is actively suppressed during saccades (*2–4*), whereas others have proposed that the visual system may simply be insensitive to the high image velocities (*5–8*). The latter is true for small features and objects, but the visual system can process image motion of 300° to 800°/s (as it occurs during saccadic eye movements) provided the features or objects are sufficiently large (*9–11*). Saccadic suppression predominantly affects the magnocellular visual system (*9*). It is particularly powerful in the motion domain (*12*, *13*) and may have evolved to blunt the startling effect of rapid visual motion that saccades would otherwise induce (*9*).

We investigated correlates of saccadic suppression in the middle temporal (MT/V5) and middle superior temporal (MST) area of the primate brain, both of which have been linked to the perception of visual motion (*14–17*). Our procedure allowed comparison of activity from directionally selective cells (MT: $n = 51$; MST: $n = 116$) [supplementary note S1 (*18*)] when visual motion was saccade induced (active condition) and when identical visual motion was induced externally (passive condition with eyes held stationary) (Fig. 1) [supplementary note S2 (*18*)]. Thirty-four of 51 (66%) cells in MT and 79 of 116 (68.1%) in MST showed significant differences [supplementary notes S3 and S4 (*18*)] between the two types of image motion. The remainder of the cells (34% in MT and 31.9% in MST) could be subdivided into two groups: (A) cells that did not respond to high-velocity image motion at all (5 MT, 15 MST cells); and (B) cells that responded equally well to the two types of motion, although with small but statistically significant latency differences [MT median latency: active 57 ms, passive 64 ms; $n = 12$, $P = 0.012$ signed rank test; MST median latency: active 63.5 ms, passive 73.5 ms; $n = 22$, $P = 0.008$, signed rank test (*19*, *20*)]. Cells of type A responded vigorously to external image motion at slow to moderate speed but were insensitive to very high image velocities such as occur during saccades. It has been proposed that this insensitivity may account for saccadic suppression (*5*, *7*, *21*). While insensitivity may contribute to the phenomenon of saccadic suppression, our results show that the majority of neurons still responded to very high image velocities, even when their speed tuning preference was shifted toward lower velocities [supplementary note S5 (*18*)]. Specific neuronal mechanisms must thus exist to achieve saccadic suppression perceptually. We hypothesized that the neural correlate of saccadic suppression would consist of neurons that simply did not respond (or responded weakly) when image motion in the preferred direction was due to a saccade, whereas they would properly signal the direction of image motion when it occurred externally ("saccadic suppression" cells). Nine of 51 cells from MT and 30 of 116 cells from MST fulfilled this criterion [supplementary notes S6 and S7 (*18*)] (Fig. 2). The average suppression for these cells was 104% in MT and 81.5% in MST (baseline activity subtracted). Psychophysical studies showed that recovery of motion sensitivity is much faster in the active than in the passive condition (*11*). This could be partly due to latency differences in the two conditions. Although the latency of most saccadic suppression neurons in the active condition could not be determined (due to suppression), some cells gave a residual response sufficient to test this hypothesis. The median latency in the active condition was 66 ms and in the passive condition 74 ms ($P = 0.055$, signed rank test, data pooled from two MT and six MST cells).

A substantial number of cells with significant differences in the active versus the passive condition showed an unexpected behavior, and we classified them as "extraretinal" cells (20 of 51 MT cells, 39 of 116 MST

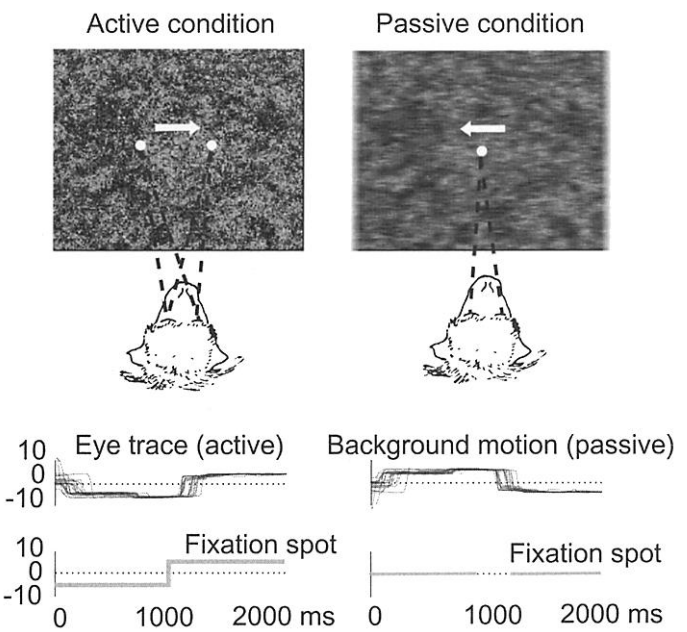

Fig. 1. Paradigm. The task consisted of an active and a passive condition. In the active condition monkeys initially fixated a spot that appeared 5° from the center. The fixation spot was displaced by 10° across the screen center at midtrial. To refixate, monkeys performed a saccade of 10°, inducing high-velocity retinal image motion. Eye position data (middle panel, left) were recorded at 1 kHz, inverted, and used to move the background in the passive condition. Here monkeys had to fixate centrally throughout the trial. The background motion was such that it generated identical retinal image motion on a trial-by-trial basis when compared to the active condition. The fixation spot disappeared (lower panel, right) midtrial for 200 ms, thus mimicking the time the monkey needed to refixate the fixation point in the active condition.

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cells). These cells exhibited saccade-induced reversal of preferred direction. Independently probed [supplementary note S5 (*18*)], they displayed a clear preferred direction that was consistent with the preferred direction they showed in the passive condition. In the active condition, extraretinal cells exhibited significantly higher activity when image motion was in the antipreferred direction (i.e., the direction of the saccade was in the preferred direction). An example of such a cell from area MT is shown in Fig. 3A. Another example (from MST) is shown in Fig. 3B. These two neurons reversed their preferred direction temporarily during saccade execution. They did not respond at all during saccades in the dark [supplementary note S7 (*18*)].

The overall effect of the reversal of preferred directions of these neurons on the population response is shown in Fig. 4A. MST population activity is plotted as a function of image motion relative to each neuron's preferred direction (upper graph). Responses to image motion in the preferred direction due to a saccade were weak and truncated early after onset, but profound when image motion was externally generated. This activity difference was significant from 80 ms after saccade onset ($P < 0.05$, Kruskal-Wallis analysis of variance, 5-ms bins). The opposite result was found for retinal image motion in the antipreferred direction (lower graph) with a strong response for the active condition and significantly weaker responses for externally induced image motion. This difference was significant from 125 ms after saccade onset. The two response functions show pronounced latency differences for the saccade-generated and the external image motion. To test the hypothesis that cells with preserved preferred directions and cells with reversed preferred directions during saccadic eye movements have different visual latencies, we assessed the neuronal visual latencies (*19*, *20*) from the direction-velocity tuning data that were independently obtained for each neuron [supplementary note S5 (*18*)]. The response onset difference in the population histogram indeed arises because MST neurons that reverse their preferred direction during a saccade on average had longer latencies to external visual motion than cells that do not show such a reversal. The means of the two groups were 87.1 and 75.5 ms (Student's t test, $P = 0.008$; medians of 85 and 75.5 ms, respectively). A similar trend was evident in our population of MT neurons, but the difference was not significant (mean latency of cells reversing their preferred direction during saccades: 69.3 ms; mean latency of nonreversing cells: 64.3 ms; $P = 0.44$; medians: 63 and 60 ms).

The saccade-related reversal of preferred directions is more readily apparent in Fig. 4B. It shows an analysis that allows for a dynamic change of preferred direction, rather than assuming it is fixed [supplementary note S8 (*18*)]. When the preferred direction remains constant, the time-resolved vectors should all point upwards (which by our definition corresponds to the preferred direction from the direction/velocity tuning). However, during saccade-induced image motion, the population vector temporarily points in the direction that is opposite to the preferred direction as determined during passive viewing.

Originally, investigators proposed that image motion during saccades was too fast to be seen (*21*), thus challenging the need for saccadic suppression. However, stimuli most effective for the motion system are seen more easily at saccade-like speeds (*22*). The latter is strong evidence for central changes of visual processing during saccadic eye movements, and we show that such changes are manifest in MT and MST. Previous studies addressing the effects of saccadic eye movements on visual processing provided somewhat equivocal results and generally failed to show direct evidence of saccadic suppression (*23*–*27*). Our data from MT and MST demonstrate that saccadic suppression is evident in a substantial fraction of direction-selective cells—they exhibit reduced activity when image motion is due to a saccade. Moreover, a subset of direction-selective cells reversed their direction tuning during saccadic eye

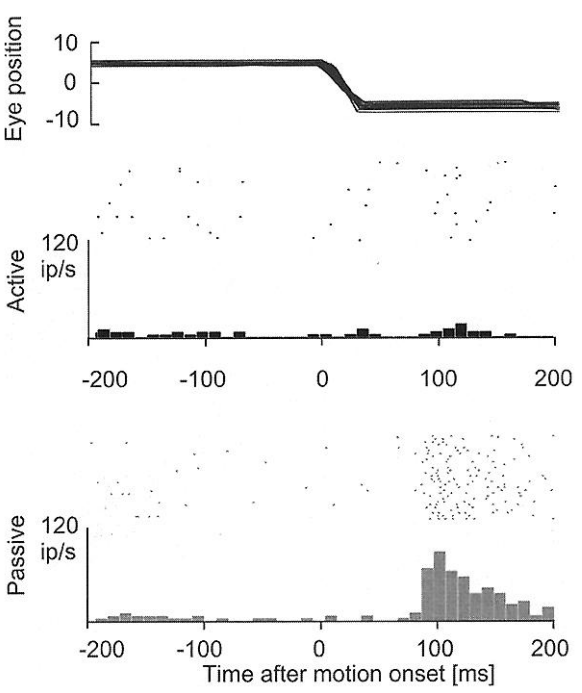

Fig. 2. Saccadic suppression cell. (Top) Horizontal eye position data aligned to saccade onset (time zero, units in degree of visual field). (Middle) Neural activity of the cell when retinal motion was due to a saccade. (Bottom) Neural activity when identical retinal image motion was due to external motion. Under these conditions, the cell responds vigorously at about 90 ms after motion onset.

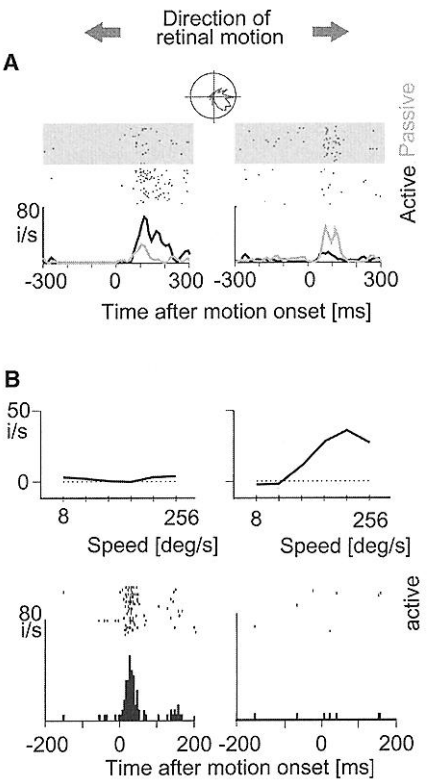

Fig. 3. Saccade-induced reversal of preferred direction. (**A**) Cell that preferred rightward motion when tested under conditions of steady fixation (small inset: directional tuning). This preference is also apparent in the passive condition (rasters in gray boxes and gray histograms). When image motion was due to a saccade, the cell responded more vigorously when image motion was to the left than to the right (black histograms and rasters on white background). (**B**) Cell that preferred rightward motion of moderate speeds [supplementary note S5 (*18*)] (upper graphs: speed tuning curves for leftward and rightward image motion). Saccade-induced image motion elicited a response only when it was in the antipreferred direction, i.e., leftward (lower histograms and rasters). The cell did not respond at all to the high image velocities in the passive condition (not shown). All responses are aligned to saccade/retinal motion onset.

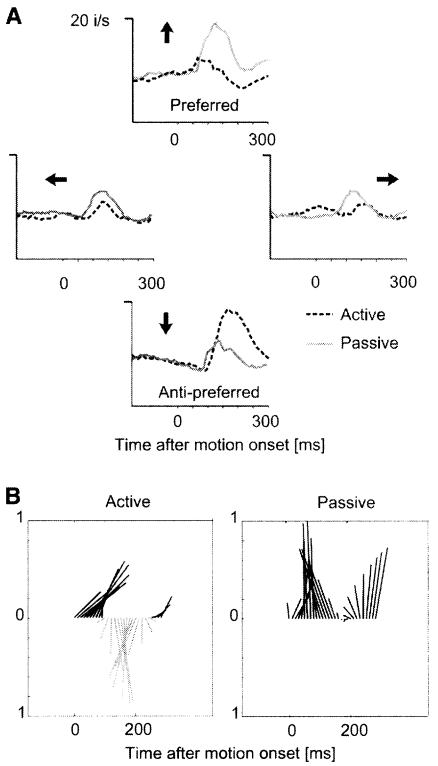

Fig. 4. Population response to saccade-induced and external motion. (**A**) Response of MST directionally selective cells as a function of direction of motion and task condition. Preferred directions of all cells are aligned and presented as upwards. Black curves show the activity when image motion was due to a saccade, gray curves the image motion when it was due to external image motion. (**B**) Time-resolved "preferred direction population vector." For each cell that contributed to (A), the preferred direction vector was calculated in 10-ms bins for the active and passive condition [supplementary note S8 (*18*)] and plotted relative to the preferred direction as determined independently [supplementary note S5 (*18*)]. The angular difference between the preferred direction assessed independently [supplementary note S5 (*18*)] and the preferred direction in the active (passive) condition determined the appearance of the direction vector in the plot. When the difference was zero the vector was plotted upwards; when it was 180° it was plotted downwards [supplementary note S8 (*18*)]. *x* axis: time (in ms) with respect to saccade (motion) onset.

movements. The activity of these neurons can be used to annul the retinal motion signal; consequently, saccade-induced motion is not perceived and external motion perception shortly after saccades is likely to be distorted (*28*). In addition, the sudden reversal of preferred motion direction demonstrates that tuning properties of cortical neurons are not necessarily static, but can be modified in the millisecond range.

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29. We are grateful to F. Bremmer and A. Welchman for valuable discussions and comments on the paper. The research was supported by Deutsche Forschungsgemeinschaft grant SFB509.

7 December 2001; accepted 18 February 2002

Cortical Neurons Encoding Path and Place: Where You Go Is Where You Are

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We recorded neuronal activity in monkey medial superior temporal (MST) cortex during movement on a motorized sled. Most neurons showed a preferred heading direction, but some responded only when that heading was part of a particular path. Others responded only when the animal was at a certain place in the room, regardless of its path to that place. Video simulations of the self-movement scene evoked path, but not place, responses. Stationary positioning in the room revealed location preferences that matched place preferences recorded during movement. We conclude that MST encodes heading, path, and place information to support visuospatial orientation.

The visual motion of optic flow (*1*) is processed by MST neurons (*2–6*) to derive the heading of self-movement (*7*). Adjacent cortical areas (*8–10*) project to hippocampal (*11*, *12*) place cells that build a cognitive map of the environment (*13–15*). This network may serve the path integration of parietal self-movement responses (*16*) involved in spatial orientation (*17*) and disorientation (*18*). We now show that MST integrates heading and location to encode the path and place of self-movement, potentially serving spatial cognition.

Natural heading sequences were presented as translational movement on a circular path in front of a stationary array of small white lights viewed during straight-ahead gaze (Fig. 1A) (*19*).

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Most MST neurons (73%, 46/63) showed significant direction tuning (Fig. 1B), identified by the circular net vector (Z of circular distribution $P \leq 0.05$) (*20*, *21*).

Clockwise (CW) and counterclockwise (CC) circular paths presented the same headings in reversed sequences with identical headings on opposite sides of the room. Nevertheless, many neurons had similar heading preferences on CW and CC paths (Fig. 1C), although 40% (25/63) showed at least a two-fold difference (*22*) between CW and CC response amplitudes (Fig. 1D).

Most neurons with comparable CW and CC response amplitudes preferred the same heading on both paths (Fig. 2A), but some preferred opposite headings. The neuron in Fig. 2B preferred rightward CW headings and leftward CC headings with both responses corresponding to the front of the room. This neuron was more affected by place-during-movement than by heading or path.

We used circular statistics (*21*) to describe heading, path, and place-during-movement selectivity. The sample's distribution of direction-