

Speed Selectivity for Optic Flow in Area 7a of the Behaving Macaque

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Area 7a, in the inferior parietal lobe, has been implicated in optic flow processing to obtain spatial information about the environment. Optic flow, angle-of-gaze and center-of-motion dependencies are already documented, but the selectivity of area 7a to speed is unknown. Such information is crucial as area 7a provides the final step in visual motion analysis that begins at the lateral geniculate nucleus and passes through MT, MST and LIP/VIP. Macaque area 7a neurons were tested with optic flows with speeds of 0.5–128°/s. Of 161 neurons tested in four hemispheres of two adult male macaques, 53% (86/161) were speed selective at either the time of stimulus onset, at the end of the trial, or at both times. Speed selectivities resembling the basic filter types (band-pass, band-reject, high-pass, low-pass, broadband) were found. Area 7a neurons exhibited two novel properties not previously reported elsewhere. Speed selectivity was found to be dynamic in that many cells gained, lost or changed speed tuning over the course of a trial. In addition, speed dependence and optic flow selectivity interacted. For example, a cell could preferentially respond to one type of navigational optic flow at a slow speed and a different navigational optic flow at a fast speed. The presence of speed selectivity combined with other properties of area 7a neurons indicates that these neurons may have a role in the concurrent representation of heading as well as multiple object speeds and directions.

Introduction

Area 7a is in the inferior parietal lobule in the dorsal or 'where' visual pathway that principally processes visual motion and maps the environment (Ungerleider and Mishkin, 1982). In humans, damage to the posterior parietal area (which includes area 7a) results in a number of visuospatial deficits such that the spatial relations between well-perceived objects are poorly perceived (Critchley, 1953; Lynch, 1980; Siegel and Read, 1997b). Area 7a has been implicated in the processing of optic flow to obtain three-dimensional information about the environment. This information includes the spatial relation of the observer to points in the environment as well as the spatial relations between different points in the environment. Cells in this area are sensitive to or selective for certain types of optic flow such as translation, expansion, compression, rotations or spirals (Sakata *et al.*, 1984, 1986; Motter and Mountcastle, 1981; Read and Siegel, 1997; Siegel and Read, 1997a). Previous work in this laboratory has demonstrated two types of optic flow selectivity in area 7a (Siegel and Read, 1997a). Some neurons were tuned to distinguish a particular type of optic flow (flow-particular or FLO-P cells, e.g. expansion versus compression), while others distinguished between different classes of optic flow (flow-general or FLO-G cells, e.g. radial optic flow versus rotational optic flow). From these studies and the finding that the optic flow tuning is constant as a function of retinotopic location (Read and Siegel, 1997), it was concluded that area 7a neurons are tuned to the global optic flow.

The selectivity to optic flow in the prior studies was tested at

only one speed, leaving open the issue of the interdependence between speed selectivity and optic flow selectivity in area 7a. Cortical inputs to area 7a come from the middle temporal area (MT or V5) via the medial superior temporal lobe (MST) and the lateral intraparietal area (LIP) (Andersen *et al.*, 1990; Cavada and Goldman-Rakic, 1989a,b; Cavada and Goldman-Rakic, 1993; Desimone and Ungerleider, 1986). Given that direct inputs to area 7a from MST and indirect inputs to 7a (e.g. from MT) possess speed selectivity (Maunsell and Van Essen, 1983; Duffy and Wurtz, 1997; Lagae *et al.*, 1993; Orban *et al.*, 1995), there are two possible re-representations in area 7a – speed invariance or speed selectivity.

A speed invariant re-representation in area 7a might be useful in representing global structure created from motion flow fields regardless of the speed of the component motions and thus allow for extraction of global structure regardless of speed (e.g. flow-global). Speed selectivity, on the other hand, would be more useful in representing speeds and distances of objects needed in order to avoid collisions and coordinate various limb movements. For example, passing a car while in traffic, pouring liquids without overflowing the cup, or grasping moving objects would require perceiving speed of, and speed changes in, the relevant optic flow.

In order to determine the representation of speed in area 7a, neuronal responses to various speeds of optic flows were recorded in four hemispheres of two adult male *Macaca mulatta*. The same optic flow stimuli used in previous studies (Read and Siegel, 1997; Siegel and Read, 1997a) were used here so that direct comparisons could be made between this study and the other studies. A rich distribution of speed tunings was found in area 7a which exhibited some novel characteristics as compared to early motion-representing regions. Furthermore it was found that the selectivity to different types of optic flow varied as a function of the speed of the display. This interaction of speed selectivity and optic flow type selectivity probably supports complex perception of changes in one's position in space, as well as changes in spatial relations within one's environment. This work has been presented in abstract form (Phinney and Siegel, 1997).

Materials and Methods

Behavioral Task

Two adult male macaques (6 and 8 kg) were required to fixate a central point and pull a lever to initiate a trial in a reaction time task (Siegel and Read, 1997a) in a dimly lit room. Two seconds after trial initiation, an optic flow stimulus appeared on the viewing screen. Monkeys needed to release the lever upon detecting a change in the optic flow stimulus that occurred randomly between 3500 and 6000 ms into the trial. Correct responses (lever release within 800 ms of the stimulus change) resulted in a 0.1 cm³ juice reward. Eye position was monitored with an infrared video camera (ISCAN Co., Cambridge, MA) and trials were aborted if eye velocity indicated a saccade. Off-line analysis confirmed fixation was

always within 1° of the fixation point. Six to 12 trials per condition were performed in all sessions in a random fixed-block sequence. Viewing distance was 57 cm and the display (Mitsubishi XC3315C monitor, VGA resolution) subtended 63°. When multiple blocks were given, the sequence of presentation was randomized from cell to cell to avoid systematic biases.

Visual Displays

The stimuli were radial compression (cmp) or expansion (exp), clockwise (cw) or counter-clockwise planar rotation (ccw), or linear translation optic flows. Translations were presented at one of eight equally spaced directions (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°). All stimuli were composed of 128 limited-lifetime white dots on a black background visible through a circular software aperture of 48° diameter (Siegel and Read, 1997a). Dot lifetime was 534 ms. Translation optic flows were presented at speeds of 2, 4, 8, 16, 32, 64 and 128°/s. Radial and rotational optic flows were presented at speeds of 0.5, 1, 2, 4, 8, 16, 32 and 64°/s. All dots moved with uniform linear velocity in the translation and radial optic flow stimuli, whereas all dots moved with uniform angular velocity in rotation optic flows, sweeping out an equal number of radians per unit time (Read and Siegel, 1997; Siegel and Read, 1997a). The angular velocity of the rotational optic flows was chosen so that average linear dot speed in the rotations approximated the uniform dot speed of the corresponding radial and translational optic flows.

The stimulus change detected by the monkey was generated in one of two ways. For radial and rotation optic flows, the start point of each vector in the display was randomly displaced within a window of 48° as points expired and were refreshed (Siegel and Andersen, 1990; Siegel and Read, 1997a). This ‘unstructuring’ destroyed the overall structure of the motion, but preserved all the trajectories and speeds. For the translations, the orientations of the vectors were randomized. This destroyed the percept of a translating field, yielding a field of randomly directed motion trajectories that contained the same statistics as the original stimulus. This stimulus differs from a random walk stimulus (Williams and Sekuler, 1984) in that a dot maintains the same trajectory (which may be curved) over its entire life.

Trials were blocked by optic flow type. For instance, a typical speed tuning block consisted of eight speed conditions (0.5, 1, 2, 4, 8, 16, 32 and 64°/s) for compression and eight for expansion, presented in a fixed-block design for eight correct repetitions per condition (128 trials). Radial optic flows were blocked together, as were rotation optic flows. Translation blocks consisted of only one direction at seven speed values (2, 4, 8, 16, 32, 64 and 128°/s). Cells were tested for optic flow selectivity and directional selectivity before speed testing. However, preliminary data indicated that a cell might prefer other speeds than the 12°/s used in the initial optic flow and direction selectivity tests. Therefore, to be rigorous and avoid any experimenter-introduced bias in the selection of optic flows, speed testing ensued even if no optic flow or direction selectivity was observed in the initial tests. If selectivity was encountered, the preferred stimulus (rotation, radial, etc.) was tested first, followed by other stimuli if time permitted. It was assumed that these cells had the same global tuning to optic flow as had been reported in area 7a (Read and Siegel, 1997; Siegel and Read, 1997a), as the large number of speed trials that needed to be run on a single cell precluded a replication of the prior results. The replication of the observation of flow-global cells supported this assumption. All cells were tested for speed tuning on at least one block (radial, or rotational, or translational optic flow) and some cells were speed tested at a number of optic flows and a number of translation directions.

Surgical and Recording Procedures

Four hemispheres of two monkeys were studied. The animals were prepared for recording using standard methods (Siegel and Read, 1997a). In brief, a recording chamber (16 mm i.d.) was placed over the posterior parietal cortex, leaving the dura intact, with stereotaxic placement as estimated from magnetic resonance imaging (MRI) data acquired just before implantation of any ferrous fittings. Coordinates of the chambers were approximately (-10AP, 18L) for all four hemispheres. Extracellular unit recordings were made with glass coated Pt-Ir electrodes (Wolbarsht *et al.*, 1960). Perpendicular penetrations through the dura were made

daily with a Kopf hydraulic microdrive. Recordings were taken from the upper few millimeters of the cortex; histological confirmation other than with the MRI has not yet been performed. These animals were concurrently used for other parietal and temporal lobe recording studies. [One monkey received 7 mg of fluoxetine hydrochloride (Prozac) p.o., 5 days a week under the direction of Rutgers University veterinarians. No difference in neuronal properties was noted between the medicated animal and the non-medicated animal.] All procedures were in accordance with Rutgers University IACUC approved procedures and with the ‘NIH Guidelines for Animals in Research’. All possible measures were taken to minimize any pain or discomfort on the part of the animals.

Statistical Analyses

Data were analyzed for all cells that yielded six or more trials per stimulus condition while most analyses were on data composed of 8–12 trials per condition.

Onset Analysis

The baseline firing rate [firing rate during the 500 ms immediately preceding the optic flow display, $M(i)_{\text{base}}$] was subtracted from onset firing rate [firing rate during the first 500 ms of the optic flow display, $M(i)_{\text{onset}}$] to yield the change in firing rate evoked by stimulus onset [$O_i = M(i)_{\text{onset}} - M(i)_{\text{base}}$] for each trial. This analysis would yield responses to the onset of the structured optic flow as compared to a display where only a red fixation point was on. Such a response (O_i) is in part due to the initial illumination of the display as well as the speed and optic flow tuning of the cell.

Across-stimulus Change Analysis

In the analysis where the response of the neurons was computed at the time that monkey was performing the detection task, a different analysis was performed. For analysis at this event, it was necessary to compare the *tonic* response to the structure motion before the change to the *evoked* response that was correlated after the change in the display from structured to unstructured motion. This was done by synchronizing the individual trials to the time that the stimulus change occurred. (Recall that the time that the stimulus change occurred was randomized in reaction time task.) The mean firing rate for the 500 ms immediately prior to the stimulus change event was computed for the i th trial [$M(i)_{\text{before}}$]. The mean firing rate was also computed for the period immediately following the stimulus change for which behavioral control was maintained [$M(i)_{\text{after}}$]. It should be stressed that this response was measured up to the time the monkey released the key. The display then turned off after the key release. Thus the response $M(i)_{\text{after}}$ was computed over a period when the stimulus was on, the monkey was fixating, and the key was being held. Typically, the monkey would release the key 300–500 ms after stimulus change so that a reasonable period could be used to estimate the firing rate. The change in the two mean firing rates were then computed [$C_i = M(i)_{\text{after}} - M(i)_{\text{before}}$] for each trial. This difference is referred to throughout the text as ‘across-stimulus change’ and thus indicates the response of the cell to the decrease in the structure of the display as well as the optic flow and the speed tuning.

Regression Procedure

Thus two different measurements of the firing rate were computed – at stimulus onset (O_i) and across stimulus change (C_i). These differences were then subjected to the stepwise least-squares linear regression procedure (SAS Co., Durham, NC; REG procedure) in log-normal space using the polynomial equation, $R_i = as_i^2 + bs_i + c + \epsilon_i$ where R_i is the cell’s change in firing rate (i.e. O_i or D_i) for the i th trial, $s_i = \log_2(\text{stimulus speed})$ in the i th trial, a and b are the regression coefficients, c is the intercept, and ϵ_i is the residual between the predicted and actual firing rate on the i th trial. If the c term alone is significant, this would indicate that the cell has an equal response to all speed conditions. If the a or b parameter is significant, this indicates that the cell is tuned to speed.

The critical value (i.e. maximum or minimum change in firing rate) occurs at $2^{-(b/2a)}$ and has the value $c - (b^2/4a)$.

Table 1 indicates how the model’s coefficients were used to define a cell’s speed tuning as band-pass, band-reject, high-pass, low-pass, non-selective or non-responsive. The definition of these terms is based upon

Table 1

Cell tunings classified by significant (+) and non-significant (-) linear regression terms

Quadratic (a)	Model coefficients		Tuning type
	Linear (b)	Constant (c)	
+	+ (-b/2a < 256°/s)	±	band-pass/band-reject
+	+ (-b/2a > 256°/s)	±	high-pass/low-pass
+	-	±	high-pass/low-pass
-	+	±	high-pass/low-pass
-	-	+	flat (broadband)
-	-	-	no tuning (non-responsive)

similar terminology in linear system theory. Cells with significant quadratic and linear terms in the model were classified as *band-pass* or *band-reject* provided the function's critical value was within the tested speed range. If it occurred outside the tested speed range, the cell was classified as *high-pass* or a *low-pass*, since the model would predict a monotonically increasing or decreasing response across all tested speeds. If the only significant term in the fit was the constant, then the response profile was termed non-selective or *broadband* because the cell responded equally to all speeds of optic flow. For the band-pass cells, the critical value was a maximum and the predicted speeds that would activate the cell by 50% of the maximum were

$$\frac{-b + \sqrt{\frac{b^2 - 4ac}{2}}}{2a} \quad \text{and} \quad \frac{-b - \sqrt{\frac{b^2 - 4ac}{2}}}{2a}$$

The bandwidth was the difference in these two values, often termed 'full width at half height' (Maunsell and Van Essen, 1983). However, this computation becomes meaningless for band-reject cells, especially if they exhibit inhibition at the critical value. For the band-reject cells, the quadratic coefficient, *a*, from the regression equation was used as a measure of the bandwidth and is compared to *a* in the band-pass functions.

For cells to which all four flows (cw, ccw, exp, cmp) and all eight speeds (0.5, 1, 2, 4, 8, 16, 32, 64°/s) were presented, the resultant '4 flow × 8 speed' experimental design was subjected to a two-way, between-subjects ANOVA. The more conservative 'between-subjects' ANOVA was used rather than the 'within-subjects' ANOVA as the former makes no assumption of correlated error across blocks. The 'between' ANOVA is therefore biased towards misses rather than false alarms in identifying selectivity. The speed and flow variables were both categorical, resulting in a general linear model. Cells were classified as (i) speed selective - flow insensitive, if only the speed variable showed significant effect at *P* < 0.05; (ii) speed insensitive - flow selective, if only the optic flow variable showed significant effect; and (iii) speed selective - flow selective. This last category was subdivided into separable effects, when a main effect of both flow type and speed was seen with no interaction, and inseparable for an interaction.

Results

A wide variety of responses to optic flows of different speed were seen in area 7a. Of the 161 cells tested, 61% showed speed selectivity to at least one optic flow type at some time in the trial. At stimulus onset, 53% (86/161) of cells exhibited speed selectivity for at least one optic flow type, 14% (22/161) were responsive but non-selective, and 33% (53/161) were non-responsive. Among the speed-selective cells were found classic band-pass response profiles, high-pass, low-pass and band-reject profiles. Figure 1 illustrates the response profiles of three selective cells exhibiting a band-pass, a band-reject and a high-pass tuning respectively. For many cells, inhibition of the firing rate relative to baseline occurred at some speeds. There was a large range of response levels, with most cells exhibiting both excitation and inhibition, some exhibiting only varying levels of

excitation, and one exhibiting only varying levels of inhibition. This representation across all the basic filter types is similar to that found in MSTd (Duffy and Wurtz, 1997).

Fifty-eight tests from 39 area 7a cells had band-pass tuning and thus the speeds that maximally and minimally activated the cells could then be determined. To quantify the relative amounts of excitation and inhibition exhibited by a cell across speeds, the minimum change in firing rate evoked by any particular speed $O(v_{min})_i$ was plotted against the maximum change in firing rate evoked by any particular speed $O(v_{max})_i$ (Fig. 2) for each speed test. (The symbol ' $O(v)_i$ ' refers to the mean rate for a particular velocity *v*.) Points which fall upon the dotted line at min = -max represent a test in which the cells exhibited roughly equal levels of excitation and inhibition. Over two-thirds (44/58) of the tests exhibited some amounts of both excitation and inhibition, appearing in the second quadrant. Many cells exhibited only varying levels of excitation (quadrant I) and one showed inhibition in both the maximum and minimum responses (quadrant III). This degree of inhibition appears to be a novel property of area 7a neurons.

Estimates of preferred speed, and bandwidths for the band-pass cells, indicate a similar speed-selectivity to that seen in MST. Figure 3A shows the plots of preferred speed versus bandwidth for the 21 neurons that were band-pass at stimulus onset. The bandwidth for band-reject cells is difficult to compute since double-height, the analogy to half-height in a band-pass cell, is difficult to determine. However, the quadratic coefficients of the band-pass and band-reject cells can be compared to see that they have similar curvature, and therefore similar tuning width (Fig. 3B). The band-pass and band-reject neurons in area 7a, like those in MST (Orban *et al.*, 1995; Duffy and Wurtz, 1997), were more broadly tuned than their counterparts in MT. Preferred speed as estimated from the polynomial fits (peak response = $-b/2a$) for the band-pass and band-reject cells was more evenly distributed across the speed continuum than in MT (Maunsell and Van Essen, 1983) where preferred speeds tended to cluster around 16-32°/s. The average preferred speed for the band-pass cells was ~24°/s versus ~8°/s for the more peaked band-reject distribution (Fig. 3C). In relation to MST neurons, speed estimates in the present study more closely resemble those of Orban *et al.* (Orban *et al.*, 1995), who report preferred speeds of 20-30°/s, than those of Duffy and Wurtz (Duffy and Wurtz, 1997), who report a predominance of high-pass cells preferring speeds of ~80°/s.

Selectivity Correlated with the Change in Structured to Unstructured Motion

In addition to the speed tuning data taken at the time of stimulus onset, speed tuning data were also computed later in the trial across stimulus change C_i . This is the change in firing rate computed across the time that the animal detects the change in structure of the stimulus (see Materials and Methods). A cell was classified as speed selective across stimulus change if it exhibited selectivity to at least one optic flow type. Of the 161 cells tested, 43 (27%) were selective (high-pass, low-pass, band-pass or band-stop) to at least one optic flow type, 54 (33%) were non-selective (broadband), and 64 (40%) were non-responsive across the time of stimulus change. Such cells were therefore selective to a reduction in the structure of the display as well as the speed.

Across the population and collapsed across optic flow type, the distribution of the type of speed tuning (i.e. untuned, high-pass, low pass, bandpass) across stimulus change was

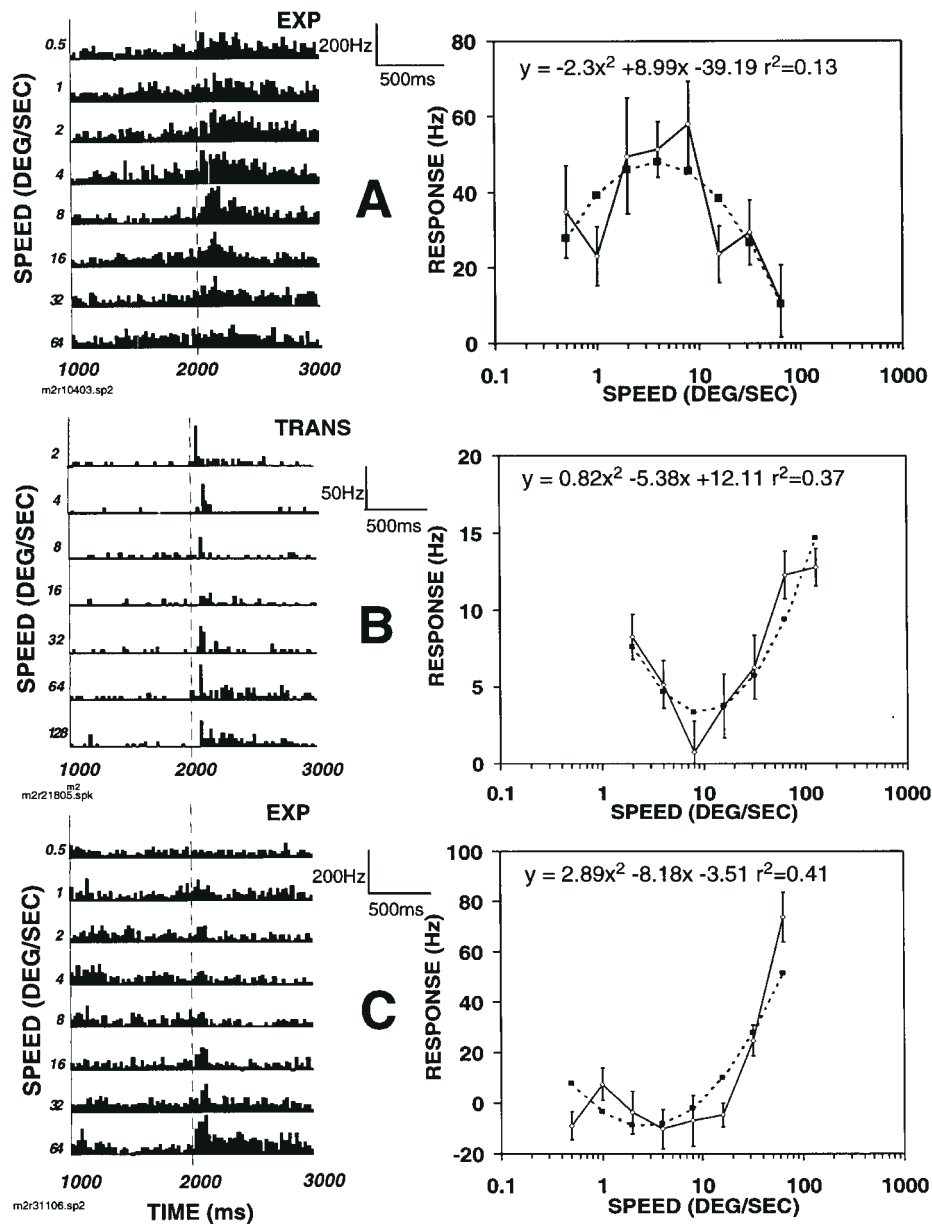


Figure 1. Peristimulus time histograms (PSTHs) and graphs of mean response amplitude for (A) a band-pass cell, (B) a band-reject cell and (C) a high-pass cell. On the left of each panel is a PSTH of the cell's response to the onset of an optic flow stimulus of different speeds. Time is on the ordinate and firing rate is indicated by histogram height. Note the scale change between panels. Maximum firing rate and timescale are indicated for each cell by a scale legend between the PSTH and the line-graph. Bin width is 25 ms. The vertical dotted line indicates stimulus onset. To the right of each histogram is a graph of the mean response amplitude for that cell, with speed on the x-axis and response strength on the y-axis. Each point represents the mean firing rate change (firing rate for 500 ms after stimulus onset minus the firing rate for 500 ms before stimulus onset) \pm 1 SEM. r^2 for the three fits shown are 0.13 ($P < 0.01$) for (A), 0.37 ($P < 0.0001$) for (B), and 0.41 ($P < 0.0001$) for (C).

altered from the time of stimulus onset (Fig. 4A). In addition, when examined on a cell-by-cell basis, a large number of cells changed speed tuning from stimulus onset to stimulus change (Fig. 4B). Of the 86 cells that were speed selective at stimulus onset (SEL column), 30 (35%) were still classified as selective across the stimulus change, 13 (15%) became speed-insensitive, and 43 (50%) had become non-responsive. Of the 22 cells that were speed-insensitive at stimulus onset (broadband) cells, six (27%) became selective, eight (36%) stayed non-selective, and eight (36%) became non-responsive when measured across stimulus change. Finally, seven (13%) of the 53 cells that were non-responsive cells (NR column) at stimulus onset became selective across stimulus change, whereas 33 (62%) became

responsive but speed-insensitive and 13 (25%) stayed non-responsive. In short, many cells underwent alterations in speed tuning as the task progressed.

The cells exhibiting no response or non-speed-selective responses at stimulus onset, but which became speed-selective by the time of stimulus change, clearly indicate that non-trivial changes in speed selectivity may occur over the course of a trial. The cells which responded when the stimulus changed, but were not speed-selective, may reflect motor or premotor processes since the animal had to release a lever at stimulus change in all cases to receive a reward. There is no way to differentiate a visually untuned response from a pre-motor response at that time in the trial. Also, the onset classification and the 'across-stimulus

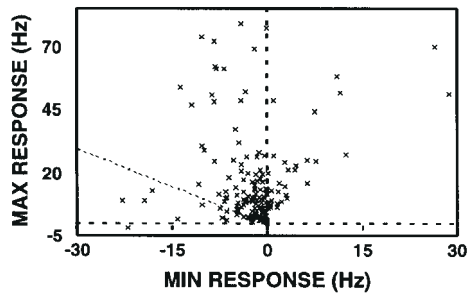


Figure 2. Inhibition index. The characteristics of the band-pass and band-reject cells were analyzed by evaluating the speed for which a minimum and maximum firing rate was obtained. Thirty-nine cells were tested with a total of 58 tests. The x-coordinate of each point is the minimum average change in firing rate of the cell (firing rate 500 ms before stimulus onset minus the rate for 500 ms after onset) and the y-coordinate is the average maximum change in firing rate of the same cell in the same test. Each point represents one test; thus a single cell may be represented by more than one point. The dotted line ($x = -y$) indicates equal strength excitation and inhibition. Points in the first quadrant indicate tests in which the cell only exhibited varying levels of excitation to different speeds of optic flow. Points in the second quadrant, which constitute the bulk of the data, indicate tests in which excitation occurred for some speeds and inhibition for others. The lone point in the third quadrant indicates a test in which only varying levels of inhibition were exhibited across speed.

change classification' may have been the result of two different speed tests. Recall that speed-selectivity was attributed to a cell when it exhibited differential response across speeds to at least one optic flow type. Thus, different speed tests may result in a cell's classification as selective at onset and selective across stimulus change.

However, there were speed-selectivity alterations in individual cells within a single optic flow type as a function of time in the trial. Figure 4C contains an example of a single neuron's differential speed tuning at 'stimulus onset' versus 'across stimulus change'. Peristimulus time histograms show the average response to a single optic flow type at two different speeds synchronized the three events in a trial – stimulus onset, stimulus change and key release. At stimulus onset there is no response to either speed stimulus. At a speed of 1°/s the cell responds vigorously to the stimulus change event. This response is not simply a motor response caused by preparation to release the lever because that response does not occur at stimulus change in the 0.5°/s condition. This cell, which exhibited no response at stimulus onset, is clearly selective by the time of stimulus change.

When the analysis of selectivity throughout the trial was restricted to a single optic flow type, most cells still changed tuning status. Figure 4D shows changes undergone by 57 of 147 cells being tested with expansion optic flows only. The cells that were always non-selective or non-responsive are not shown. In this case, selectivities were broken down into filter types (band-pass, band-reject, high-pass, low-pass, etc.). Note that even the neurons that were selective at both stimulus onset and across stimulus change tended to show different types of selectivity (e.g. high-pass at onset and band-pass at change). Only two cells maintained the same type of selectivity (e.g. high pass at both onset and change) over the course of a trial. Similar distributions of speed-tuning changes over the trial were found for the other optic flows.

Interaction of Speed and Optic Flow at Time of Stimulus Onset

A number of cells exhibited speed selectivity to more than one optic flow type. Of the 161 cells in this study, 141 cells were

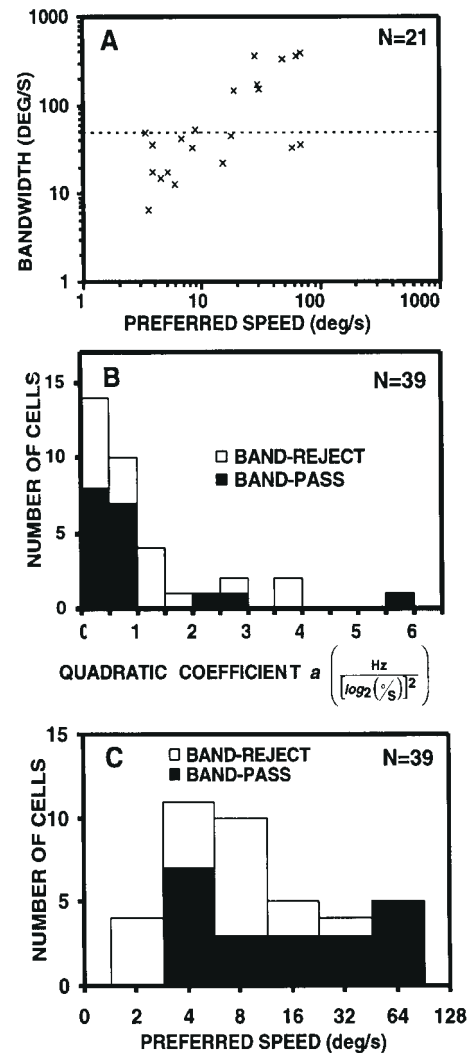


Figure 3. Preferred speeds and bandwidths of speed selectivity in area 7a neurons. (A) Preferred speed versus bandwidth for neurons exhibiting band-pass tuning at stimulus onset. The dotted line is at a 50°/s bandwidth, which Lagae *et al.* (Lagae *et al.*, 1993) used as the demarcation between band-pass and broadband classifications. In the present study, the degree of curvature (a coefficient from the model) is used to define band-pass since the size in degrees per second should increase with increasing preferred speed. (B) Histograms comparing the quadratic coefficients of the band-pass versus band-reject cells. The distributions are quite similar, indicating that their bandwidths are similar. (C) Bar graph of preferred speed as estimated from the polynomial fits ($-b/2a$). The height of the histogram indicates the number of cells whose polynomial fit reached a maximum at that speed labeled under the bar. Across the band-pass and band-reject cells, 16–32°/s are the most commonly preferred speeds (note the 'preferred' speed for a band-reject cell would be the speed at which minimal response, or maximal inhibition, occurred).

tested at multiple speeds with more than one optic flow. Of those 141 cells, 48 were speed-selective to more than one optic flow (e.g. 315° translation and expansion). Fifty-three of the 141 cells were fully tested for expansion, compression, clockwise rotation and counterclockwise rotation – the cardinal directions in spiral space (Graziano *et al.*, 1994). The results of these individual speed tests for each optic flow type were subjected to a two-way ANOVA with optic flow type (expansion, compression, clockwise rotation and counter-clockwise rotation) and speed (0.5, 1, 2, 4, 8, 16, 32, 64°/s) as the two factors (see Materials and Methods). About one-quarter of the cells (14/53)

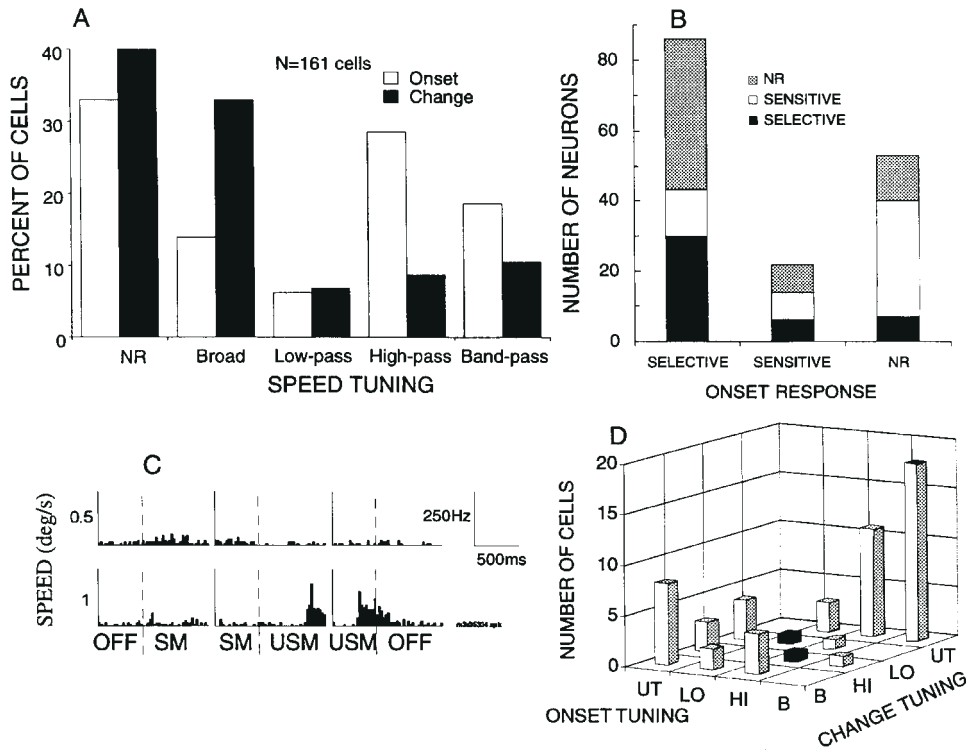


Figure 4. Speed tuning changes from time of stimulus onset to time of stimulus change. (A) Population distribution of band tunings at stimulus onset and across stimulus change. The population tuning shifts from a predominantly high-pass tuning at stimulus onset to a more even distribution of low-pass, high-pass and band-pass cells measured across stimulus change. (B) Distribution of speed selective, sensitive and non-responsive cells at stimulus onset and stimulus change. The height of each bar represents the number of cells that displayed that tuning type at stimulus onset. The colored sections within each bar indicate the number of those cells that exhibited a selective tuning (white), a non-selective (broadband) tuning (hatched) or no response (black) at the time of stimulus change. (C) Changes in selectivity between two times within a trial for a single neuron at two different speeds. Peristimulus time histograms (PSTHs) of a single neuron's responses to two different speeds at the time of stimulus onset (left), at the time of stimulus change (middle) and at the time of lever release (right). The cell's response to the two speeds is identical at stimulus onset, but varied at stimulus change. The effect at the time of stimulus change cannot be due to premotor (lever release) issues since there is no response at 0.5°/s even though lever release occurs at the same time in a trial for both speeds. Bin width is 25 ms. (D) Tuning modulations evaluated with the expansion optic flow stimuli. A group of 57 neurons exhibited speed selective responses at either stimulus onset, across stimulus change, or both. Speed tuning at stimulus onset is represented (onset tuning) on the axis at left. The axis at right represents tunings at stimulus change (change tuning). The height of each column represents the number of cells that fell into that classification. The 90 cells that were untuned to expansion optic flow throughout the entire trial (UT → UT) are not shown. Fifteen neurons (10%) were untuned at stimulus onset but became tuned by stimulus change (UT → HI, UT → LO, UT → B). Thirty-two neurons (20%) were tuned at onset but became untuned by stimulus change (LO → UT, HI → UT, B → UT). On the diagonal lie the two cells (colored black) which maintained tuning (LO → LO and HI → HI). All others (8/149 or 5%) represent cells which were speed selective both at onset and at stimulus change, but differed in the type of tuning (LO → HI, LO → B, HI → LO, HI → B, B → LO, B → HI). (HI = highpass, LO = lowpass, B = band-pass or band-reject, UT = untuned, e.g. UT → LO denotes cells which were untuned at stimulus onset and low-pass at stimulus change.)

had significant optic flow and speed-selective factors. Of these cells, six showed separable selectivities – i.e. speed selectivity and optic flow selectivity but no interaction – and eight showed inseparable selectivities – i.e. an interaction between speed and optic flow selectivities. This group of 14 cells underwent changes in optic flow selectivity as a function of dot speed in the display. Optic flow selectivity alone with no speed selectivity was seen in 17% (9/53), and speed selectivity alone was seen in 11% (6/53) of the cells. Forty-five percent (24/53) of the cells were insensitive to both speed and optic flow changes. However, 14 of these 'non-sensitive' cells did show selectivity or sensitivity to one or more of the individual tests when fit by the quadratic function. It may be that the variance between tests was large enough to obscure speed or optic flow tuning for these cells. This variance may have been due to the 1–2 h period needed to collect the different tests.

Figure 5 shows radar plots of the average response of four cells to the four optic flow types (expansion, compression, clockwise rotation and counterclockwise rotation) at each of eight speeds (0.5, 1, 2, 4, 8, 16, 32, 64°/s). For each speed tested the optic flow tuning is shown in spiral space (Graziano *et al.*, 1994). The

distance along each axis of the radar plot indicates the strength of response to the optic flow assigned to that axis. Thus speed selectivity is seen in changes of plot size and shape across plots, optic flow selectivity is indicated by uneven aspect ratio of individual plots, and their interaction is seen here as changes in the area and the aspect ratio across the plots. In addition to cells that altered their optic flow selectivity as a function of speed, some cells were speed invariant but optic flow selective, while others were speed selective but invariant to optic flow type. The former may be examples of flow-general cells; the latter may simply signal the average speed in the display.

In summary, speed selectivity, optic flow selectivity, modulation of those selectivities and interactions between them were seen in area 7a neurons. Very few individual cells maintained the same tuning as the trial progressed. Many cells dramatically gained, lost or changed their speed selectivity between the time of stimulus onset and the time of stimulus change. In addition, speed selectivity was found to interact with optic flow selectivity in either separable or inseparable effects in an individual neuron.

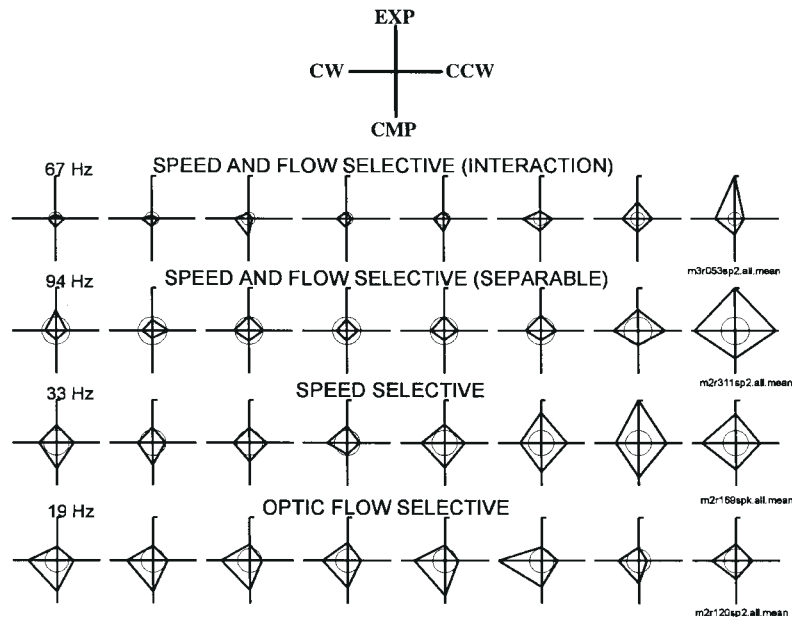


Figure 5. Spiral space diagrams of optic flow selectivity at different speeds. The response of four cells to four optic flows at eight speeds are graphed, one cell per line. Each line contains average responses of a single neuron at eight different speeds (0.5, 1, 2, 4, 8, 16, 32 and 64°/s) to each of four different optic flows (expansion, compression, clockwise rotation and counter-clockwise rotation). For each diagram, the distance from the center along a given axis indicates the cell's response strength for the optic flow represented along that axis. Thus the distance along the positive *x*-axis indicates expansion response magnitude, positive *y*-axis distance denotes clockwise rotation response magnitude, negative *x*-axis distance denotes compression response magnitude, and negative *y*-axis distance denotes counter-clockwise rotation response magnitude. The thick-lined diamond indicates the firing rate of the cell for 500 ms after stimulus onset. The circle indicates the baseline response of the cell (average firing rate 500ms before stimulus onset). The axes of each line are normalized to the maximum response of that cell. The number at the top of the left most plot on each line indicates the maximum response represented by the extent of the axes. (A) A cell exhibiting optic flow selectivity and speed selectivity with an interaction. (B) A cell exhibiting optic flow selectivity and speed selectivity with no interaction. (C) A cell exhibiting speed selectivity and no optic flow selectivity. (D) A cell exhibiting optic flow selectivity and no speed selectivity. (EXP = expansion, COM = compression, CCR = counter-clockwise rotation, CWR = clockwise rotation.)

Discussion

Speed Tuning Characteristics of Area 7a Neurons

The recordings demonstrate that neurons in area 7a are selective to the speeds of optic flow. Over half of cells tested were speed selective at some time in the trial. These selectivities cannot be attributed to any other parameter than speed as all stimulus parameters except speed (dot life, density, brightness, mean speed, display size, etc.) were held constant within a block. Many of the area 7a cells showed inhibition as a function of speed. Cells were found with speed selectivities representing all the major filter types (e.g. high-pass, low-pass, band-pass, band-reject, broadband), although band-pass and band-reject tuning predominated. The bandwidths were somewhat broader than those found in MT but similar to those found in MST.

A number of neurons in area 7a were selective for a combination of both speed and optic flow and these selectivities could interact or be separable. The interaction of speed and optic flow tuning implies that adequate characterization of a cell's response to environmental optic flow, which may vary in speed, requires testing at several speeds. Presumably this distribution of speed and optic flow selectivities across cells allows for a complete representation of speeds and moving forms while still allowing abstraction of speed from the global form from the composite speeds.

Speed selectivity seen in area 7a neurons was dynamic and could be altered as the trial progressed. The speed tuning was evaluated at two time points. The tuning at the stimulus onset, when the display illuminates the screen, and there is a particular optic flow at a particular speed, was measured. The tuning

across the stimulus change, when the structure in the display decreases, and there is a particular unstructured motion at a particular speed and the monkey is planning to release the key, was also measured. In making the speed tuning comparison across the two events, it is necessary to note that there are multiple differences in the two events. The present work is unable to distinguish whether the observed modulation in speed tuning is purely due to attentional mechanisms or is due to stimulus variables that differ between stimulus *onset* and stimulus *change*. However, in area 7a there are changes in visual properties that are clearly attributable to attentional or behavioral state changes at different times within a trial, for optic flow (Siegel and Read, 1997a) and for receptive field size and shape (Bushnell *et al.*, 1981; Steinmetz *et al.*, 1994). We suggest that this also may be the case for the modulation of optic flow speed selectivity in area 7a.

Comparison to Speed Selectivity in Other Cortical Areas

MT appears to extract basic motion parameters in a retinotopic representation. It is also tuned to motion contrasts and seems more sharply speed and direction tuned than V1 (Snowden *et al.*, 1992). In addition, MT also seems to process more complex motion stimuli including transparency (Snowden *et al.*, 1991) and velocity gradients (Allman *et al.*, 1985; Treue and Andersen, 1996). Thus, MT may be providing a basis set for motion representation. Additional motion processing occurs in MST in which fully fledged optic flow selectivity for translations, radial motions and rotations are seen (Duffy and Wurtz, 1991; Orban *et al.*, 1992; Graziano *et al.*, 1994). In addition to the classic band-pass and broadband speed-selective cells found in MT, MST

also possesses cells with band-reject speed tunings (Duffy and Wurtz, 1997).

The preferred speeds and bandwidths of cells in area 7a were found to be in rough agreement with measurements in MST. Most 7a cells were either band-pass or band-reject with average preferred speeds of 24 and 8°/s respectively. Maunsell and Van Essen (Maunsell and Van Essen, 1983) found MT cells to prefer ~32°/s, whereas Lagae *et al.* (Lagae *et al.*, 1993) found preferred speeds to be nearer 10°/s. In MST, Orban *et al.* described 14 cells which exhibited mainly band-pass speed selectivity to complex optic flow, preferring speeds of 20–30°/s (Orban *et al.*, 1995). Duffy and Wurtz found much higher preferred speeds, often ~80°/s, with high-pass speed selectivities more prevalent than the band-pass or band-reject tunings which predominate in 7a (Duffy and Wurtz, 1997). Thus, area 7a is like MT/MST in that it has similarly tuned band-pass cells. However, the presence of band-reject, high-pass and low-pass cells suggest properties derived from MST (Duffy and Wurtz, 1997)

The speed tunings found in the present study encompassed all the basic filter types – band-pass, band-reject, high-pass, low-pass and flat (broadband). This rich representation of the different filter types has also been found in MSTd (Duffy and Wurtz, 1997). In contrast, MT and V1 exhibit only band-pass, flat, low-pass and non-responsive tunings (Lagae *et al.*, 1993; Maunsell and Van Essen, 1983). It may be that the two areas beyond MT compute and use the band-reject outputs to enhance psychophysical performance beyond that allowed by band-pass channels alone. These new representations may also serve to increase the information content (Linsker, 1990). Neurons in area 7a differed from those in MT/MST in that they often exhibited inhibition of response rates below baseline over substantial portions of the tested speed range. This increased appearance of inhibition in area 7a neurons may arise from the neural computation of differences of the speed tuning of MST neurons.

Both area MST and 7a neurons change their speed tuning as a function of optic flow. Thus, in MST a neuron may exhibit different speed tuning to a navigational optic flow and a translation (Orban *et al.*, 1995). In area 7a similar cells are seen, but a new group of cells is also observed (e.g. Fig. 5) for which speed tuning may vary for the different types of navigational optic flow. The modulation of navigational optic flow tuning by speed that is reported here occurs on a cell-by-cell basis. These single-cell changes may have arisen from different demands upon the visual system when at rest or moving. Body, head and limb movements lead to different distributions of optic flows and speeds across the retina. For example, when a monkey is stationary, many of the self-generated retinal motions that arise from head, trunk and limb movements will be translations and planar rotations at lower velocities. While a monkey is locomoting, either through brachiation or running, the speeds will be higher and tend to be combinations of expansion and translations. Independently moving objects generate additional visual processing demands (e.g. a small radius, high-speed expansion indicates an approaching object which may require evasive action). It is possible that the speed-dependent alterations in the optic flow tuning across the population of area 7a neurons may have evolved to match these ecologically based information processing needs. Current models of motion processing have not reported such malleability in the speed and optic flow tuning of their processing units (Cameron *et al.*, 1998; Zemel and Sejnowski, 1998) and may need to be modified to better simulate primate higher motion processing.

In conclusion, the neurons of area 7a exhibit novel optic flow selectivities (Read and Siegel, 1997; Siegel and Read, 1997a). Cells are present in area 7a, which respond to general types of optic flow regardless of direction (flow-general cells) as well as those selective for a particular type of flow (flow-particular). Other parameters that alter optic flow selectivity in area 7a are speed (present work), eye position (Read and Siegel, 1997) and disparity (Phinney and Siegel, 1998). The combination of optic flow and other stimulus and motor selectivities with speed selectivity allows a novel representation of object and observer speeds and relative positions as compared to V1, MT or MST. In addition to these static properties, the sensory responses of some area 7a neurons are dynamic across the trial, and may be modulated by attentional or behavioral factors. This might indicate that area 7a neurons mark which components of a flow field are attentionally relevant or require a response. Thus, area 7a is probably combining information from multiple stimulus dimensions to provide computation of self-motion, object motion, time to impact and heading perception – all of which are crucial elements in the representation of extrapersonal space and may be used for motor planning. These data, combined with known motion representations in human parietal cortex (Bonda *et al.*, 1996), and psychophysical studies (Cornilleau-Peres, 1997), further implicate area 7a as crucial in the representation of extrapersonal spatial relationships from motion.

Notes

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