

Responses to direction and transparent motion stimuli in area FST of the macaque

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Abstract

Motion transparency occurs when multiple object velocities are present within a local region of retinotopic space. Transparent signals can carry information useful in the segmentation of moving objects and in the extraction of three-dimensional structure from relative motion cues. However, the physiological substrate underlying the detection of motion transparency is poorly understood. Direction tuned neurons in area MT are suppressed by transparent stimuli, suggesting that other motion sensitive areas may be needed to represent this signal robustly. Recent neuroimaging evidence implicated two such areas in the macaque superior temporal sulcus. We studied one of these, FST, with electrophysiological methods and found that a large fraction of the neurons responded well to two opposite directions of motion and to transparent stimuli containing those same directions. A linear combination of MT-like responses qualitatively reproduces this behavior and predicts that FST neurons can be tuned for transparent motion containing specific direction and depth components. We suggest that FST plays a role in motion segmentation based on transparent signals.

Keywords: FST, MT, Transparent motion, Motion opponency, Motion segmentation

Introduction

Motion transparency refers to the perception of more than one object velocity within a local region of retinotopic space (Snowden et al., 1991; Qian et al., 1994). It occurs frequently in natural settings, for example, when moving objects partially occlude each other or when a shadow drifts across a textured background. Because it tends to occur near the boundaries of moving objects, it contains information that may be useful for image segmentation. It also arises under conditions where relative motion cues are used to compute three-dimensional (3D) structure—the so-called kinetic depth effect (Wallach & O'Connell, 1953; Bradley et al., 1998; Dodd et al., 2001; Giese & Poggio, 2003). In the laboratory, transparency is typically studied using two superimposed dot patterns moving in different (usually opposite) directions (Snowden et al., 1991; Qian et al., 1994; Qian & Andersen, 1994; Bradley et al., 1995; Curran et al., 2007). Perceptually, these stimuli appear as two patterns drifting across each other, indicating that the visual system can represent more than one motion signal within a local retinotopic area (Qian et al., 1994).

The physiological mechanisms underlying the detection of transparent motion remain unclear. Local, spatially segregated

estimates of an object's velocity tend to differ so the pooling of a number of these measurements is often required to accurately estimate velocity. However, spatial pooling can blend different motion signals together, causing them to begin to cancel. This is advantageous for motion noise reduction but poses a problem for the detection of transparent motion (Qian & Andersen, 1994; Born & Bradley, 2005). A number of computer vision algorithms designed to analyze moving images epitomize this problem. These algorithms often implement a pooling or regularization stage which results in every point in the scene being assigned a single velocity, thus precluding the detection of transparent motion (Hildreth, 1984; Heeger, 1987; Poggio et al., 1988; Grzywacz & Yuille, 1990). Similarly, MT neurons (which also pool direction signals spatially) are suppressed when a pattern moving in a non-preferred direction is added to one moving in the preferred direction (Snowden et al., 1991; Qian & Andersen, 1994; Recanzone et al., 1997; Treue et al., 2000). An analogous effect is found if the two patterns are segregated spatially but both located within a neuron's receptive field (Snowden et al., 1991; Bradley et al., 1995). This suppression is typically referred to as motion opponency (it is strongest when the components move in opposite directions) and is believed to reflect MT's role in filtering out motion noise, in part because V1 neurons are not substantially affected by the addition of an opponent motion pattern (Snowden et al., 1991; Qian & Andersen, 1994, 1995; Born & Bradley, 2005). The suppressive effect of transparent motion on MT implies that the neural representation of

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transparency may be highly distributed (cf., Treue et al., 2000) and that motion sensitive areas other than MT may be involved.

Recent evidence from an fMRI study suggested that two areas in the superior temporal sulcus (STS), the fundus of the STS (FST) and the lower superior temporal region (LST), are strongly activated by opponent motion patterns (Nelissen et al., 2006). This raises the possibility that individual neurons in these areas are selective for transparent motion with components moving in opposite directions. To investigate this hypothesis, we recorded from one of these areas, FST, which lies immediately anterior to and receives a large direct projection from MT (Desimone & Ungerleider, 1986). In particular, we were interested in comparing the responses of FST neurons to direction and transparent motion stimuli. We found that about 35% of the recorded neurons were *axially tuned*, responding strongly to two opposite directions but weakly driven by the orthogonal directions. In general, FST neurons responded about the same to transparent stimuli containing two opposite directions and to either of the components alone (indicating a lack of motion opponency). This contrasts with the finding of strong motion opponency in MT and MST, one of MT's primary projection sites (Ungerleider & Desimone, 1986; Snowden et al., 1991; Recanzone et al., 1997). These results provide one of the first quantitative analyses of electrophysiological data in FST and, to our knowledge, reveal the existence of a previously unidentified class of neuron in the STS which lacks motion opponency. We also present a simple model for these neurons in which a linear combination of the output of direction and disparity selective MT neurons is computed. The model qualitatively reproduces our experimental results and leads to the prediction that FST neurons can be tuned for transparent signals with specific direction and depth components. We suggest that FST is involved in motion segmentation based on transparent signals.

A preliminary report of these results was previously presented (Rosenberg et al., 2007).

Materials and methods

Subjects and surgery

Data presented in this paper were gathered from three awake behaving adult rhesus monkeys (*Macaca mulatta*), two male and one female. Prior to the experiments, each animal was equipped with a cylindrical stainless steel recording chamber (placed supradurally over a craniotomy positioned at 17 mm lateral, -4 mm anterior in stereotactic coordinates) and a scleral search coil to monitor eye position (Judge et al., 1980). All surgical procedures were conducted under deep anesthesia using isoflurane. These surgical methods have been detailed previously (Evarts, 1966). All surgical and experimental protocols complied with US Department of Agriculture (USDA) and National Institutes of Health (NIH) guidelines for the humane care, and use of laboratory animals and were approved by the University of Chicago Internal Animal Care and Use Committee (IACUC).

Experimental procedures and electrophysiological recording

Extracellular action potentials were recorded from 72 neurons in the STS: 41 from MT and 31 from FST. MT recordings were gathered from all three monkeys and FST recordings from one of the male monkeys. During recording sessions, a monkey was seated comfortably in a custom-built primate chair 57 cm in front of a

stimulus display system in a shielded recording room. Recordings were conducted with single epoxy-coated tungsten microelectrodes with impedances between 0.1 and 2 M Ω (diameter = 200 μ m, FHC Inc., Bowdoin, ME) that were advanced dorsoventrally.

Neurons in MT were identified by known physiological properties including strong direction selectivity, localized receptive fields confined to the contralateral visual field, receptive field sizes that scale with eccentricity, anatomical depth, and relative location to MSTd (Born & Bradley, 2005). We verified that the receptive field parameters (size and location in visual space) at different recording sites matched the known topography of MT (Gattass & Gross, 1981; Maunsell & Van Essen, 1983a). FST neurons were identified based on their anatomical position and physiological properties. As expected anatomically, our estimates of the FST recording sites based on penetration parameters were confined about 1–5 mm anterior to MT (Desimone & Ungerleider, 1986; Nelissen et al., 2006). The retinotopic organization we observed is consistent with FST but not MT, LST, or either of the MST areas (Nelissen et al., 2006). Parafoveal receptive fields were found in the most posterior recordings and were about 4° in diameter at an eccentricity of 1–2°. The receptive fields of the most anterior neurons covered more peripheral portions of the visual field and were 20° in diameter or larger at an eccentricity of about 10–15°. These measurements are consistent with a previous report of the relationship between eccentricity and receptive field size in FST (Desimone & Ungerleider, 1986). As reported in that study, we also found that some FST receptive fields extended into the ipsilateral hemisphere. Further, FST receptive fields were roughly twice as large as those in MT were at a given eccentricity (Desimone & Ungerleider, 1986) and much smaller than those in STP which typically cover almost the entire visual field (Oram et al., 1993).

In addition to anatomical position and receptive field parameters, the responses of FST neurons to direction, transparent motion, and optic flow stimuli provide additional criteria for distinguishing the area from others in the STS. First, only a minority of FST neurons are direction selective (about 10% in our sample). On the other hand, essentially all MT neurons, about 70% in MSTv, and about 50% in MSTd are direction selective (Saito et al., 1986; Komatsu & Wurtz, 1988; Eifuku & Wurtz, 1999; Born & Bradley, 2005). Second, a large proportion of FST neurons are axially tuned (about 35% in our sample), responding strongly to two opposite directions of motion. In contrast, this is observed in about 1% of MST neurons (Saito et al., 1986) and 4% of STP neurons (Oram et al., 1993). Third, unlike neurons in MT and MST (Snowden et al., 1991; Recanzone et al., 1997), we found that FST neurons generally lack motion opponency. Finally, we found no indication that FST neurons are selective for optic flow stimuli, differentiating the area from MSTd.

The extent and location of receptive fields of isolated single units were estimated using dot patterns and bars that were manually moved on the presentation screen. Having established the retinotopic location, the approximate extent of the receptive field, and estimated direction selectivity, we proceeded with the experimental conditions. Action potential waveforms were triggered using a threshold and sampled at 40 kHz. For the majority of neurons, full waveforms were stored from 200 ms pre-trigger to 800 ms post-trigger for later offline sorting. The OfflineSorter software (Plexon Inc., Dallas, TX) was used to perform conservative offline sorting using principal components analysis to emphasize the isolation of stable single units. Some neurons were isolated using a window discriminator and firing rates and variances were calculated from spike times.

Visual stimuli and behavioral task

We used random dot kinematograms (RDKs) with 100% motion coherence (direction stimuli) and transparent motion stimuli consisting of two unpaired dot patterns moving in either opposite or orthogonal directions within the zero disparity depth plane (Snowden et al., 1991; Qian & Andersen, 1994). For these stimuli, the number of dots drifting in each direction was equal. Optic flow stimuli (contractions, expansions, and rotations) were also presented. For all stimuli, the dot density was three dots per square degree and each dot had a diameter of 0.1° with a luminance of 42 cd/m^2 (background 2 cd/m^2). The dots appeared and disappeared asynchronously at random positions with a lifetime of 200 ms. The high dot density of the stimuli saturates the responses of both V1 and MT neurons, so differences in direction and transparent motion responses are not likely due to the difference in number of dots translating in a fixed direction (Snowden et al., 1991, 1992).

At the start of each trial, a monkey was given 1 s to begin fixating a dot on the screen. After fixation onset, there was a 300 ms delay before the presentation of the stimulus, which lasted another 500 ms. The fixation point was then extinguished and a liquid reward was delivered if fixation was maintained within 1° around that point. If fixation was broken prematurely, the trial was immediately aborted and the data for that trial were excluded from further analysis.

Data analysis

Two tuning indices were calculated using the empirically measured, non-baseline subtracted direction tuning curves. The first was a standard direction tuning index (DTI), Eq. (1). The term R_θ is the firing rate for the preferred direction and $R_{\theta-180}$ is the firing rate for the opposite (anti-preferred) direction. Values near one indicate strong direction tuning while values near zero indicate no direction tuning.

$$DTI = \frac{R_\theta - R_{\theta-180}}{R_\theta + R_{\theta-180}}. \quad (1)$$

The second index compares the strength of responses along the preferred motion axis defined by R_θ and $R_{\theta-180}$ against those along the orthogonal axis. We refer to this measure as the axial tuning index (ATI), Eq. (2). The terms $R_{\theta-90}$ and $R_{\theta+90}$ are the responses to the directions orthogonal to the preferred motion axis. Values near one indicate strong axial tuning while values near zero indicate non-axial tuning. Note that the ATI can be negative for direction tuned neurons if $R_{\theta-180}$ is small.

$$ATI = \frac{(R_\theta \times R_{\theta-180}) - (R_{\theta-90} \times R_{\theta+90})}{(R_\theta \times R_{\theta-180}) + (R_{\theta-90} \times R_{\theta+90})}. \quad (2)$$

To estimate the angle between the preferred directions of a bimodally tuned FST neuron, we defined an analytical function using the first five terms (including DC) of the Fourier series expansion of its direction tuning curve and then measured the angle between the peaks of this function.

Modeling

We modeled the responses of axially tuned FST neurons using an approach similar to the basis function method formulated by Pouget and Sejnowski (1997). The goal of this type of model is to

reproduce the activity of one class of neuron (the output layer) by operating on stereotyped models of the responses of their presynaptic neurons (the input layer). The first step is to construct tuning curves for the input layer that match those observed physiologically. The second is to determine a set of operations that transform the responses of the input layer into those of the output layer. Matching known anatomical relationships (Ungerleider & Desimone, 1986), the input layer of our model represents MT neurons and the output layer represents axially tuned FST neurons.

To model MT direction tuning, we used the von Mises distribution (circular Gaussian), Eq. (3). Gaussians are frequently used to fit experimentally measured MT direction tuning curves (e.g., Albright, 1984; Britten & Newsome, 1998; DeAngelis & Uka, 2003) and a polar coordinate system is used because direction of motion is periodic. Here θ is the independent variable (direction of motion), θ_0 sets the preferred direction, and κ determines the tuning bandwidth. To reproduce a physiologically realistic bandwidth, κ was set to 1.62 in the simulations.

$$Dir_{\theta_0}(\theta) = e^{\kappa \cdot \cos(\theta - \theta_0)}. \quad (3)$$

In addition to being direction tuned, many MT neurons are selective for binocular disparity or depth (Maunsell & Van Essen, 1983b). To model depth tuning, we used a Gaussian over a linear space representing horizontal disparity (with units of degrees), Eq. (4). MT disparity tuning curves can take several forms, but a large percentage of them are well described by the Gaussian function (DeAngelis & Uka, 2003). Here x is the independent variable (disparity), x_0 sets the preferred disparity, and σ_x sets the tuning bandwidth. Consistent with Gaussian fits to experimental data (DeAngelis & Uka, 2003); σ_x was set to 0.51 in the simulations.

$$Disp_{x_0}(x) = e^{-(x-x_0)^2/(2 \cdot \sigma_x^2)}. \quad (4)$$

Calculating the response of a model MT neuron to a stimulus moving in direction θ_i at disparity x_i begins with the product of its *direction* and *disparity* tuning curves evaluated at those arguments, Eq. (5). If the stimulus contains multiple components at different directions or disparities, the sum of responses to each component is taken.

$$MT_{\theta_0, x_0}(\theta, x) = Dir_{\theta_0}(\theta) \cdot Disp_{x_0}(x). \quad (5)$$

Motion opponency is then introduced by subtracting the weighted response of a model MT neuron whose tuning is the same except for preferring the opposite direction of motion, Eq. (6). This is consistent with the finding that MT neurons are typically most suppressed when the components of a transparent stimulus move in opposite directions at the same disparity (Bradley et al., 1995). As a result of this setup, the disparity tuning bandwidth determines how the magnitude of motion opponency falls off as the relative disparity between transparent components increases. Specifically, the model predicts that motion opponency will fall off more slowly for neurons with broader disparity tuning. Consistent with experimental data (Bradley et al., 1995), when $\sigma_x = 0.51$ there is a 15% reduction in activity when a stimulus at the preferred direction and disparity is paired with one moving in the opposite direction at a disparity 0.75° away. This step also has the slight effect of sharpening the direction tuning. Here $[\cdot]_0$ denotes half-wave rectification and W_j is a weighting coefficient chosen to reproduce a physiologically realistic level of motion opponency. In the simulations, $W_j = 0.48$, resulting in a 45% reduction in activity when a

stimulus moving in the preferred direction and disparity is paired with one moving in the opposite direction and same disparity (Snowden et al., 1991; Qian & Andersen, 1994).

$$MT_{\theta_0, x_0}(\theta, x) = [MT_{\theta_0, x_0}(\theta, x) - W_I \cdot [MT_{\theta_0-180, x_0}(\theta, x)]]_0 \quad (6)$$

We then assume a simple transformation between MT and axially tuned FST neurons, in which a linear combination of the output of two MT neurons preferring opposite directions of motion (θ_0 and θ_0-180) and disparities (x_0 and x_1) is computed, Eq. (7). In the simulations presented, the preferred directions are left and right and the preferred disparities are -0.69° and 0.75° , respectively. Here θ^\dagger and x^\dagger are vectors, emphasizing that the stimulus can contain more than one direction and disparity.

$$FST_{\theta_0-180, x_0, 1}(\theta^\dagger, x^\dagger) = [MT_{\theta_0, x_0}(\theta^\dagger, x^\dagger) + MT_{\theta_0-180, x_1}(\theta^\dagger, x^\dagger)]_0 \quad (7)$$

In simulations not presented, the weighted activity of MT units preferring directions orthogonal to the preferred motion axis of the model FST neuron was subtracted off before rectification. Depending on the weighting term, the tuning either sharpened or broadened, reproducing the range of behaviors we observed. However, doing so did not change the main results and required additional parameters not well characterized at this time. Also, since FST receptive fields are larger than those in MT at a given eccentricity, an actual FST neuron would need to sum over two pools of MT neurons whose receptive fields together cover an extended retinotopic area.

Results

Experimental findings

We encountered heterogeneous tuning across neurons in FST. About 35% (11/31) were axially tuned, responding strongly to two opposite directions of motion but weakly to the orthogonal directions (Figs. 1A, 1B). For these neurons, the estimated angle between the preferred directions was within $5.82^\circ \pm 3.52^\circ$ (mean and standard deviation) of 180° . For comparison, other groups have found that about 4% of neurons in STP and 1% in the MST areas show similar axial tuning (Saito et al., 1986; Oram et al., 1993). The high prevalence of axial tuning in FST thus seems to distinguish the area from others in the STS. About 35% (11/31) of the FST neurons in our sample were broadly tuned for direction, not showing a strong preference for either a single direction or axis of motion (Fig. 1C). However, these neurons often had a small axial bias (e.g., Fig. 1C), as reflected in moderate ATI scores (Fig. 2B). The remaining 29% of neurons (9/31) showed a variety of other response properties including direction tuning (3/31), bimodal tuning in which the angle difference between the preferred directions was not 180° (2/31; they were 125° and 149°), or amorphous/non-responsive direction tuning (4/31). One broadly tuned neuron in our sample responded more strongly to an optic flow stimulus (contraction) over the maximum direction response. However, using the responses to the contraction stimulus and the best direction as arguments for the DTI, it was concluded that the neuron was not selective for optic flow (DTI = 0.06).

The FST and MT populations could be distinguished using the DTI and ATI scores from the two areas. The mean DTI was 0.20 ± 0.04 SEM in FST and 0.74 ± 0.02 SEM in MT (Fig. 2A). This

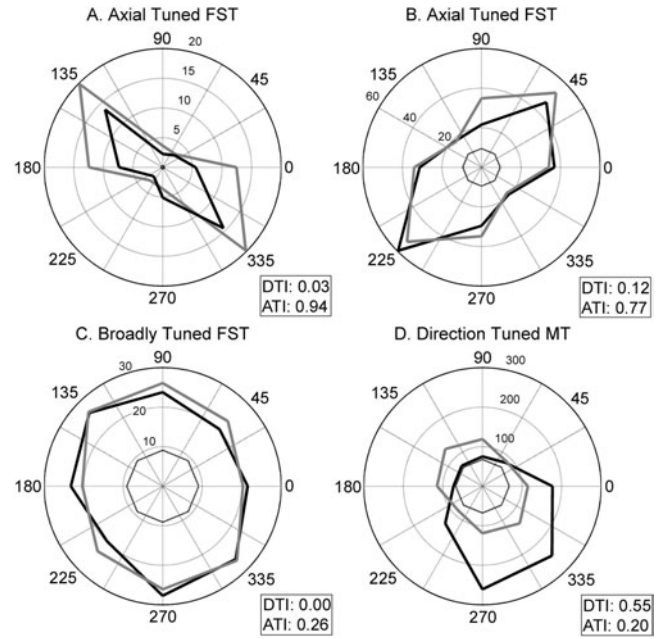


Fig. 1. Example Tuning Curves from Neurons in Areas FST and MT. (A) Strongly axially tuned FST neuron. (B) Moderately axially tuned FST neuron. (C) Broadly tuned FST neuron. (D) Direction tuned MT neuron. Solid black lines are direction tuning, finely dotted black lines indicate baseline, and solid gray lines are transparent motion tuning (transparent responses are plotted twice, once at each of the component directions).

difference is statistically significant ($p < 0.001$, t -test), indicating that direction tuning is stronger in MT than in FST. The mean ATI was 0.42 ± 0.06 SEM in FST and 0.11 ± 0.06 SEM in MT. This difference is also statistically significant ($p = 0.001$, t -test), indicating that axial tuning is stronger in FST than in MT (Fig. 2B). While the responses of many FST neurons to opposite directions of motion were similar, they were not identical. For the axially tuned neurons, the ratio of R_θ to $R_{\theta-180}$ ranged between 1.05 and 1.46. On average, R_θ was about 18% greater than $R_{\theta-180}$ for axially tuned neurons and 24% greater for broadly tuned neurons. When determining the size and location of receptive fields, we also observed (but did not systematically quantify) that the receptive fields of axially tuned neurons were spatially homogeneous, responding well to two opposite directions at all locations.

Transparent motion tuning curves with components moving in opposite directions were gathered for 18 FST neurons. Overall, the response magnitudes were similar for transparent motion and direction stimuli (cf., Figs. 1A–1C). The responses of an MT neuron to these stimuli are also presented to illustrate the effect of motion opponency (Fig. 1D). For the axially tuned neurons, the mean ratio of the transparent motion response along the preferred motion axis to the average of the responses to the two component directions was 0.96 (median = 1.01). For the broadly tuned neurons, the result was similar—the mean ratio was 1.08 (median = 1.01). A scatter plot of the preferred transparent motion responses versus the averaged responses to the two component directions for 16 FST neurons responsive to direction stimuli is presented in Fig. 3. The slope of the best fitting line through these data is 1.04, further illustrating that FST neurons lack motion opponency. The transparent motion and direction tuning curves of the axially tuned neurons were also highly similar in shape—the median correlation between them was 0.9.

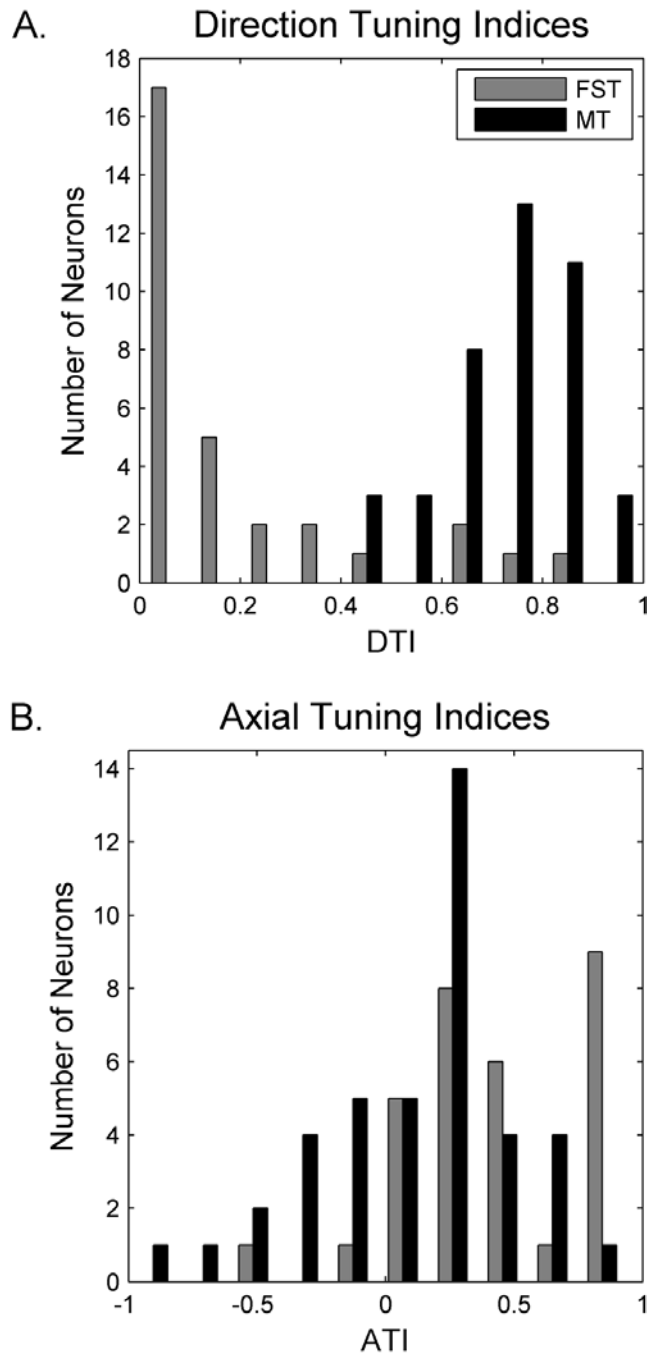


Fig. 2. Distribution of Direction and Axial Tuning Indices. (A). Histogram of the direction tuning index (DTI) for 31 neurons recorded in FST and 41 neurons recorded in MT. The average DTI was 0.20 in FST and 0.74 in MT. (B) Histogram of the axial tuning index (ATI). The average ATI was 0.42 in FST and 0.11 in MT. Negative ATI scores result when a neuron has a strong preferred direction response, a weak anti-preferred direction response, and moderate responses to the orthogonal directions.

For two of the axially tuned FST neurons, transparent motion stimuli with components moving in orthogonal directions were also presented. The addition of an orthogonal direction to either of the preferred directions resulted in a strong reduction in firing rate, $53\% \pm 4\%$ mean and SEM (two neurons \times two preferred axial directions paired with an orthogonal direction). This result, al-

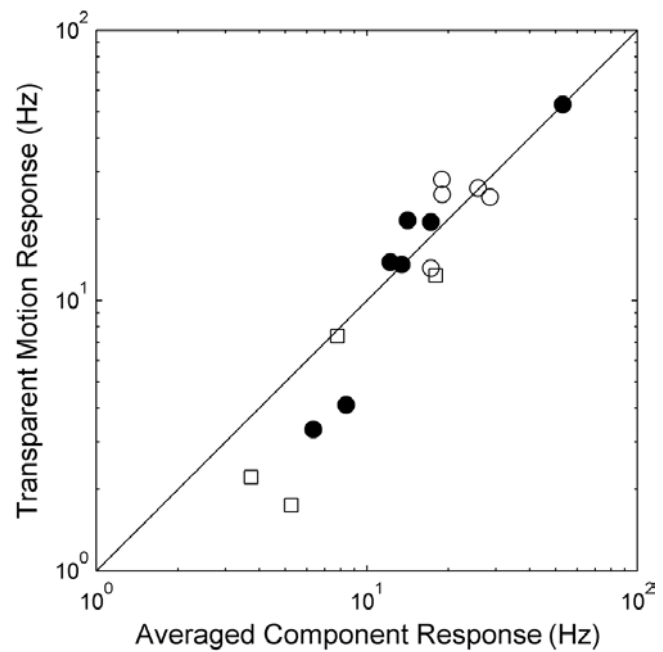


Fig. 3. Comparison of Direction and Transparent Motion Responses in Area FST. Preferred transparent motion responses are plotted against the averaged responses to the two direction components for 16 FST neurons. The solid line is unity (the slope of the best fitting line through the data is 1.04), filled circles are axially tuned, open circles are broadly tuned, and squares are unimodal, bimodal off-axis, or amorphously tuned neurons.

though limited by sample size, suggests that unlike MT neurons which are most suppressed by opponent motion, axially tuned FST neurons are most suppressed by directions orthogonal to the preferred motion axis.

Modeling results

We constructed a simple model positing that axially tuned FST neurons compute a linear combination of the output of a small population of MT neurons. A schematic describing how axially tuned FST receptive fields may be constructed from the output of MT neurons is presented in Fig. 4A. The model qualitatively reproduces our experimental findings and responds preferentially to a transparent stimulus with components moving in opposite directions and different disparities.

One of the MT units was set to prefer leftward motion and disparities closer than the fixation plane (-0.69°) while the other was set to prefer rightward motion and disparities further than the fixation plane (0.75°). The responses of the leftward tuned unit to direction and transparent stimuli (with components moving in opposite directions) within the zero disparity depth planes are presented in Fig. 4B. Consistent with experimental data (Snowden et al., 1991; Qian & Andersen, 1994), the addition of the opponent pattern reduces the preferred direction response by 45% (compare to Fig. 1D). The responses of the FST unit to the same stimuli are presented in Fig. 4D. The responses are similar, but not equivalent, to opposite directions of motion because the MT units are not equally driven by zero disparity stimuli (due to the difference in their preferred disparities). This demonstrates the prediction that the strength of axial tuning measured for an FST neuron will

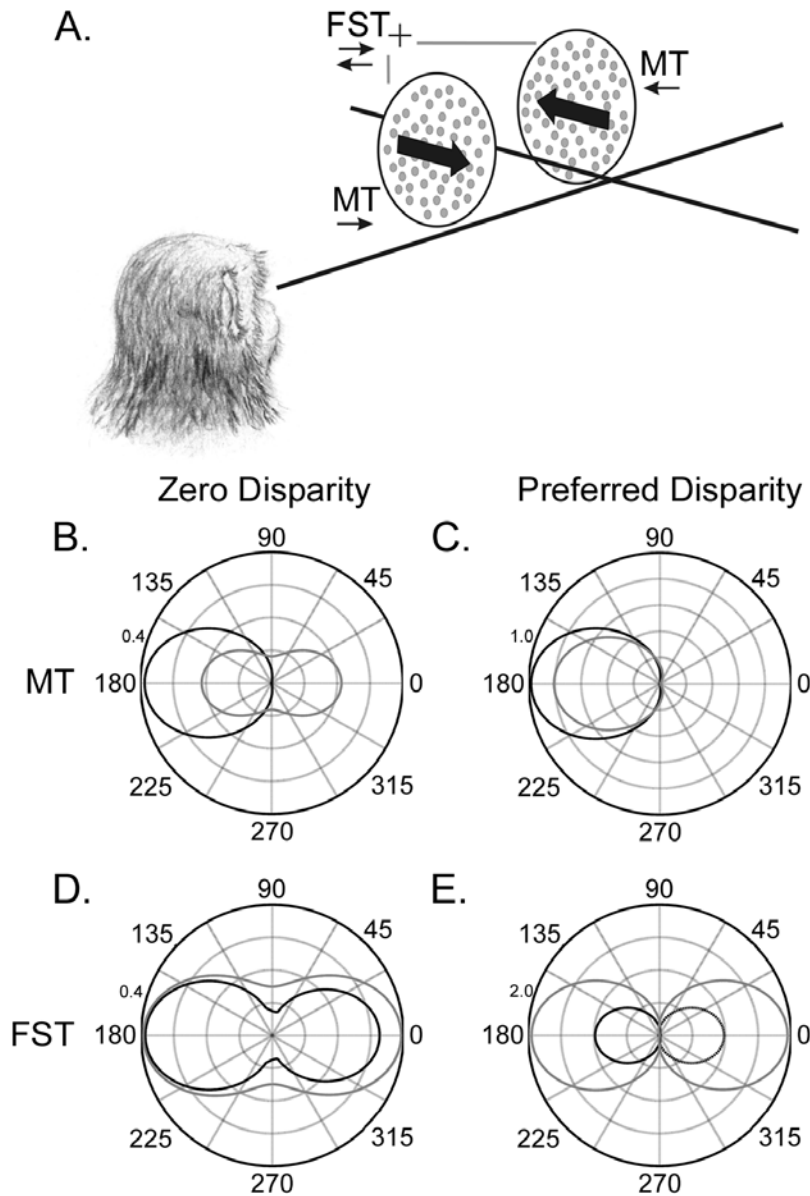


Fig. 4. A Model of Axially Tuned FST Neurons. (A) Schematic of the model. An axially tuned FST neuron integrates the output of MT neurons whose receptive fields have similar retinotopic locations but prefer opposite directions and different disparities. The disparity preferences of the MT neurons are depicted on opposite sides of the fixated frontoparallel plane but they could both lie on either side of that plane. (B, C) Direction (black lines) and transparent responses (gray lines) of a model MT neuron tuned for leftward motion. (B) Direction stimuli and both components of the transparent stimuli are at zero disparity. Transparent responses are plotted twice as in Fig. 1. (C) Direction stimuli and one component of the transparent stimuli are at the unit's preferred disparity while the opponent (transparent) pattern is at a disparity 0.69° away. Note that separating the components in depth reduces the magnitude of motion opponency. The transparent motion tuning curve has only one lobe because the unit does not respond to transparent stimuli containing both a component at the preferred depth but moving at an angle close to the anti-preferred direction and one component at the non-preferred depth but moving at an angle close to the preferred direction. (D, E) Direction (black lines) and transparent responses (gray lines, plotted twice as in Fig. 1) of a model FST neuron tuned for the left-right motion axis. (D) Direction stimuli and both components of the transparent stimuli are at zero disparity. Note that the direction responses are similar (but not equal) to opposite directions of motion, as well as the similarity between the direction and transparent motion responses. (E) Two direction tuning curves (solid and finely dotted black lines) were calculated, one at each of the disparities preferred by the model MT neurons. The transparent motion tuning curve was calculated with a component at each of those disparities. Note the disparity dependent reversal in direction preference and that the transparent responses are larger than the direction responses.

depend on the disparity of the direction stimuli and how well that disparity activates the neuron's two (hypothetical) MT pools. The neuron will appear direction tuned when tested with stimuli that drive only one of the MT pools but will be axially tuned when tested with stimuli that drive both pools (see also Fig. 4E). This may explain the heterogeneity of direction responses we found in FST, including direction tuning, variability in the ratio of R_θ to $R_{\theta-180}$ for axially tuned neurons, and broadly tuned (with some axial bias) neurons which may have been poorly driven by zero disparity stimuli. For the model FST neuron, the ratio of the transparent motion response along the preferred motion axis to the average of the component responses was 1.1. This is larger than the experimental average of 0.96 but is similar to the average of 1.14 obtained when neurons with weaker preferred transparent responses than averaged component responses were excluded.

In MT, motion opponency is often greatly reduced when the opponent direction pattern has a different disparity than the preferred direction pattern (Bradley et al., 1995). Separation in depth

by about $\pm 0.8^\circ$ frequently reduces suppression to about 10–20%. For the MT units in the model, motion opponency is reduced to 15% when the opponent stimulus is located 0.75° from the preferred disparity. The responses of the leftward tuned MT unit to direction stimuli at its preferred disparity are presented in Fig. 4C. Also presented are the unit's responses to transparent stimuli with one component at the preferred disparity and an opposite going component 0.69° away. Note that the direction responses are maximized and that motion opponency has been greatly reduced (cf., Fig. 4B). This reduction in motion opponency may have important implications for the responses of axially tuned FST neurons. Specifically, by taking the linear combination of two pools of MT neurons that prefer opposite directions and sufficiently different disparities (such that the effects of motion opponency are relatively weak when a transparent stimulus with components at the preferred disparities of the two pools is presented), an FST neuron would respond better to the appropriate transparent stimuli than to any direction stimulus. In other words,

the responses of axially tuned FST neurons could specifically signal the presence of transparent motion. To demonstrate this, the responses of the FST unit to two sets of direction stimuli, one at each of the preferred disparities of its input units, and to transparent stimuli with a component at each of those disparities (and moving in opposite directions) are presented in Fig. 4E. Because the magnitude of motion opponency suppressing the MT units is small, the transparent motion responses of the FST unit are larger than the direction responses. Also note that the FST unit appears direction tuned when tested with either set of direction stimuli, but that the preferred direction reverses with disparity.

Discussion

In FST, we found a large subpopulation of neurons selective for opposite directions of motion. While this type of tuning has been observed in a small percentage of neurons in the MST areas and STP (Saito et al., 1986; Roy et al., 1992; Oram et al., 1993), this is the first report showing that it is common within a single extrastriate area. These neurons were observed to respond well to two opposite directions of motion at all locations within the receptive field. Furthermore, motion opponency was largely absent; the neurons responded roughly the same to a transparent stimulus with components moving in opposite directions within the zero disparity depth plane as to either of the components presented alone. This finding is atypical in the STS, and differentiates the area from neighboring motion sensitive regions such as MT and MSTd.

The prevalence of direction selective cells in our FST data set differs somewhat from a previous report (Desimone & Ungerleider, 1986). Several factors may account for this difference: First, our study was conducted in awake behaving monkeys in which stimuli were presented binocularly. In contrast, Desimone and Ungerleider (1986) used paralyzed anesthetized monkeys and presented stimuli monocularly. Second, our study emphasized the isolation of single units and the use of quantitative measures of direction selectivity, rather than a qualitative (audible difference in firing rate) characterization of multi-unit responses. A third, but less likely, reason for this difference is that the studies were conducted in different subspecies of macaque.

Detecting transparent motion

We found that direction and transparent stimuli (with components moving in opposite directions within the zero disparity depth planes) elicit highly similar responses from neurons in FST. It would thus be difficult to differentiate between these stimuli using the responses of FST neurons alone. In MT, a different problem hinders the detection of transparent motion. As the acute angle between two components of a transparent stimulus increases, the MT population response becomes increasingly dual peaked (Treue et al., 2000); however, the amplitudes of these peaks also diminish (and are minimized at 180°), reducing MT's ability to reliably signal transparency. Interestingly, we found in FST that the majority of bimodal direction tuned neurons preferred directions 180° apart. This bias may reflect a compensatory mechanism acting to offset the suppressive effects of motion opponency, establishing a network that uses the joint activity of FST and MT to more reliably signal transparency. When there is a large angle difference between components (roughly $\geq 125^\circ$, the minimum angle difference between the preferred directions of an FST neuron in our sample), transparency could be signaled by a large response in FST and two

small responses in MT. When components have a smaller angle difference ($<125^\circ$), two distinguishable responses in MT and two in FST could signal transparency. A trade-off in the relative activity between areas that depends on the angle between the transparent components may be reflected in our observation that the preferred direction responses of axially tuned FST neurons were suppressed by the addition of an orthogonal direction. Finally, a single direction could be identified by a single large response in each area. This setup is similar to a "ratio model", such as those suggested to account for the perception of speed (Thompson, 1982; Krekelberg et al., 2006).

Comments on the model

Our modeling results suggest that axially tuned FST neurons could be most active when the components of a transparent stimulus have different disparities (for example, when viewing an animal moving behind bushes on a windy day). This prediction is consistent with the psychophysical finding that transparency is more salient when the relative disparity between components is greater (Qian et al., 1994; Greenwood & Edwards, 2006) and the physiological finding that some FST neurons are strongly activated by motion defined depth structure with components moving in opposite directions (Mysore et al., 2007). It also implies that these neurons may be selective for transparency signals containing specific pairs of components, which support a recent psychophysical argument that the components of transparent stimuli are processed simultaneously (Curran et al., 2007).

This prediction is based on the hypothesis that an axially tuned FST neuron linearly combines the output of two pools of MT neurons that prefer opposite directions of motion and disparities that are different enough that the preferred stimulus of either pool only weakly inhibits the other. Anatomically, this is possible (Ungerleider & Desimone, 1986) and its plausibility is supported by the finding that FST is involved in extracting 3D structure from motion cues (including selectivity for motion defined depth structure with components moving in opposite directions), which implies the integration of multiple directions as well as depths (Sereno et al., 2002; Vanduffel et al., 2002; Nelissen et al., 2006; Mysore et al., 2007). Furthermore, the finding that the ratio of the preferred transparent motion response to the average of the two component responses was distributed around one is expected from the linear combination of two pools of MT neurons since transparent motion responses in MT are roughly half the strength of direction responses (when the components move in opposite directions within a single depth plane). This setup ostensibly limits the range of disparity pairs that FST neurons could represent, however, in MT there is variability both in the magnitude of motion opponency and how far apart in depth two components must be before motion opponency relaxes (Snowden et al., 1991; Qian & Andersen, 1994; Bradley et al., 1995). The selective integration of MT neurons according to these properties could therefore increase the range of disparity pairs represented in FST.

Future work and implications

Further work is needed to systematically test the relationship between direction and disparity tuning in FST. For one, a comparison of disparity tuning curves calculated using stimuli moving in opposite directions along the preferred motion axis is needed. The prediction is that the peaks of these tuning curves will be well segregated. Direction tuning curves calculated at the peaks of these

disparity tuning curves are expected to peak in opposite directions. Further tests are also needed to confirm that axially tuned FST neurons are typically suppressed by directions orthogonal to the preferred motion axis.

Our results suggest that axially tuned neurons in FST may work cooperatively with MT in order to improve the detection of transparent signals. These neurons may also specifically signal certain cases of transparency, particularly when the components move in opposite directions. Transparency detectors selective for components moving in opposite directions would be useful in parsing objects within a dynamic visual scene and in extracting 3D structure from motion cues (e.g., see Giese & Poggio, 2003; Nelissen et al., 2006). We suggest that axially tuned FST neurons serve as the neurophysiological substrate of these detectors and consequently that they play an important role in motion segmentation based on transparent signals. Interestingly, our prediction that axially tuned FST neurons will show a disparity dependent reversal in direction preference was previously observed in MSTd but not MSTv (Roy et al., 1992; Eifuku & Wurtz, 1999). Together, these results suggest that the pooling of oppositely direction tuned MT neurons in a disparity specific fashion may be a common strategy used by the visual system in solving motion problems.

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