SFN 2013
306.22

Characterization of primate visual cortex responses to local motion signals: Fourier, non-Fourier, and glider

E.I. Nitzany, Q. Hu, A. Schmid, Y. Yu and J.D. Victor
Brain and Mind Institute, Weill Cornell Medical College, New York, NY

Motivation and Background

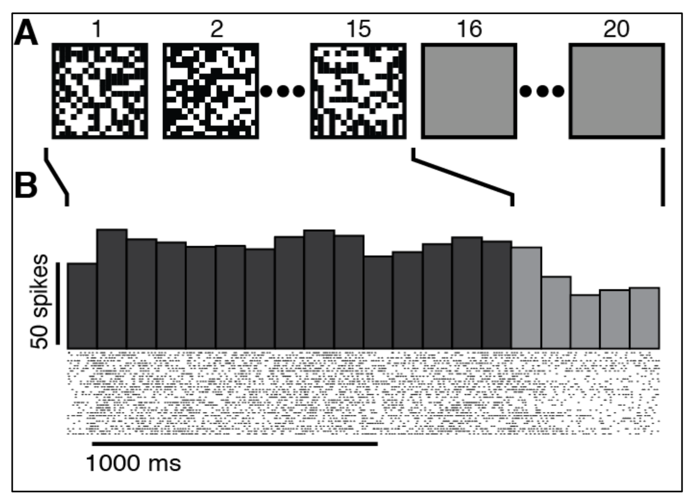
Analysis of motion is critical to many visual tasks, such as segregating objects from background and navigating through space. Motion analysis is generally considered to begin with an initial stage in which local motion signals are extracted. Two kinds of local motion signals are well-recognized: Fourier (F) signals, which consist of simple spatiotemporal correlation (Reichardt 1961), and non-Fourier (NF) signals, which consist of spatiotemporal correlation of an elementary feature, such as an edge or flicker (Chubb & Sperling 1988). More recently, a third kind of local motion signal, glider (G) motion, was identified (Hu & Victor 2010). G motion consists of third- and higher-order correlations in a slanted spatiotemporal region; it can be produced by local expansions and contractions, even in the absence of F or NF signals. All three kinds of local motion signals are present in naturalistic stimuli (Nitzany & Victor, CoSyNe 2012). Here, we determine the sensitivities of V1 and V2 neurons to these three kinds of motion.

Method

Physiology: Single-unit recordings using multitetrode arrays were made in V1 and V2 of 13 macaques , anesthetized with propofol and sufentanil, and paralyzed with vecuronium or rocuronium. In most cases, recording sites were determined from histological identification of lesions and tracks.

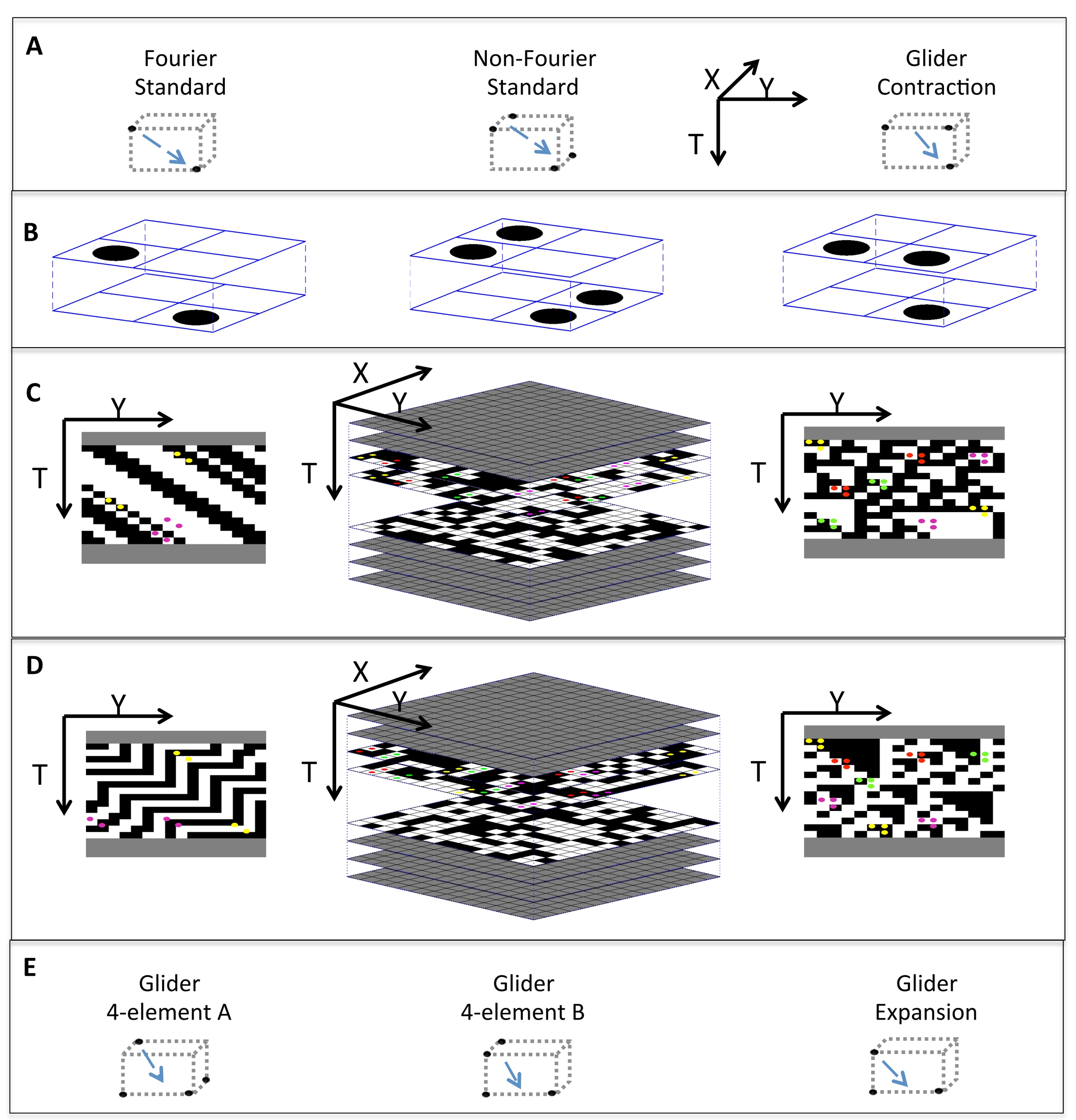
Data analysis: Spike sorting: After bandpass filtering (300 to 9000 Hz) and thresholding, waveforms were clustered using custom versions of KlusterKwik and Klusters (Hazan et al, 2006). Features consisted of peak amplitudes and principal components.

Visual stimuli: Stimuli were constructed by concatenating segments (illustrated below – Panel A) that contained examples of one of the three kinds of motion (see below). Segments consisted of 15 frames (100 ms each) of a 16 x 16- array of black and white checks, and were separated by 500 ms of a constant gray background. The size of the check and the orientation of the array was determined by optimizing the response to an easily-isolated neuron in the recorded cluster.



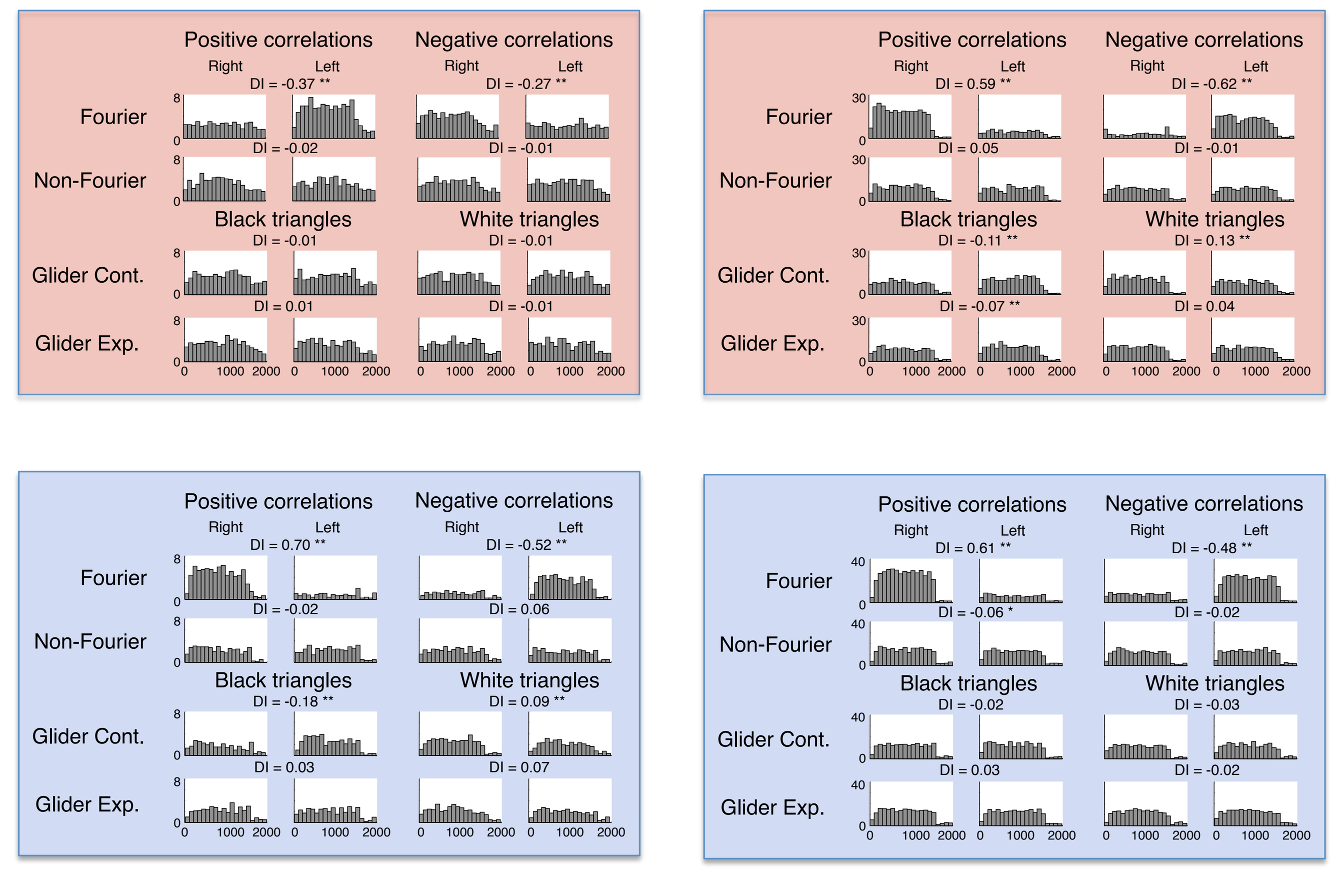
For each kind of motion, several subtypes were tested: positive and negatively-correlated Fourier (F) motion, positively- and negatively-correlated non-Fourier (NF) motion, and glider (G) motion based on white (G-W) or black (G-K), triangles, expanding or contracting. In each case, segments containing motion in opposite directions were presented sequentially. A total of 12 such segment pairs were presented in a block-randomized order, along with a segment with no motion, for a total of 25 segments. This sequence was repeated 32 times, for a total duration of 26 min. Four such sequences, each with different exemplars of the motion types, were presented. Analysis was based on the spike counts for the period between 50 to 1600 ms of each segment (see Panel B).

Stimulus construction: Panels A and B: Each kind of motion corresponds to a correlation rule inside a space-time template of checks. For Fourier (F) motion, the array is a pair of checks on a diagonal in space-time. For non-Fourier (NF) motion, the template consists of a parallelogram of four checks – here, two checks sharing an edge at one time, and then shifted in position at the next time. For glider (G) motion, the template consists of three checks in a spatiotemporal triangle. A spatiotemporal movie is synthesized by requiring that the total number of black checks inside the template is an even number (panel C), or an odd number (panel D); see colored dots for examples. When the number of black checks in a glider is even (panel C), this results in standard Fourier motion (first column), or motion of a spatial edge (middle column), or contraction of white triangles (right column). When the number of black checks in a glider is odd (panel D), this results in a reverse-phi Fourier motion stimulus (left column), a reversed-phi non-Fourier stimulus (middle column), or contraction of black triangles (right column). Further variants can be constructed based on other glider shapes and orientations (Panel E). Note that for NF and G stimuli, pairwise correlations to motion (Fourier cues) are absent. Moreover, NF stimuli do contain G cues, and G stimuli do not contain NF cues. For further details, see Hu & Victor (Journal of Vision, 2010).



Results

Examples of individual neuron responses



Example neurons (V1: upper panels, V2: lower panels) demonstrating typical motion sensitivities. Neurons in both areas were sensitive to all kinds of motion; many neurons were sensitive to more than one kind. The directional index (DI) and its significance (* for p<0.05, ** for p<0.01, *** for p<0.001) is shown above the PSTH's of responses to each pair of opposing stimuli.

Calculating indexes

Directional Index (DI) score

For each type of motion, direction selectivity was quantified by a direction index (DI), given by

$$DI = \frac{M_{right} - M_{left}}{M_{right} + M_{left}}$$

where M_{right} and M_{left} are the mean firing rates for stimuli in the two opposing directions over the period 50 to 1600 milliseconds following stimulus onset. Significance was determined by a t-test (paired, two-tailed) across 25 trials containing the given motion type.

Motion Complexity (MC) score

To determine whether motion responses were consistent with an opponent mechanism, we defined a "motion complexity" (MC) score:

$$MC = \sum_{m \in \{F,\ NF,\ G-\exp,\ G-cont\}} \left| DI(m,+) + DI(m,-) \right|$$

The rationale for this index is that under the hypothesis that motion responses are generated by an opponent mechanism, the DI should invert when the parity of the motion signal inverts – i.e., when positive correlations are replaced by negative correlations. Thus, if motion type *m* is extracted by an opponent mechanism, then DI(*m*,+)=-DI(*m*,+), and the contribution of the *m*th term to the MC score zero. That is to say, for a MC score that is greater than zero, responses to positive and negative correlations are inconsistent with an opponent mechanism.

For the example on the right the MC score is calculated as follows:

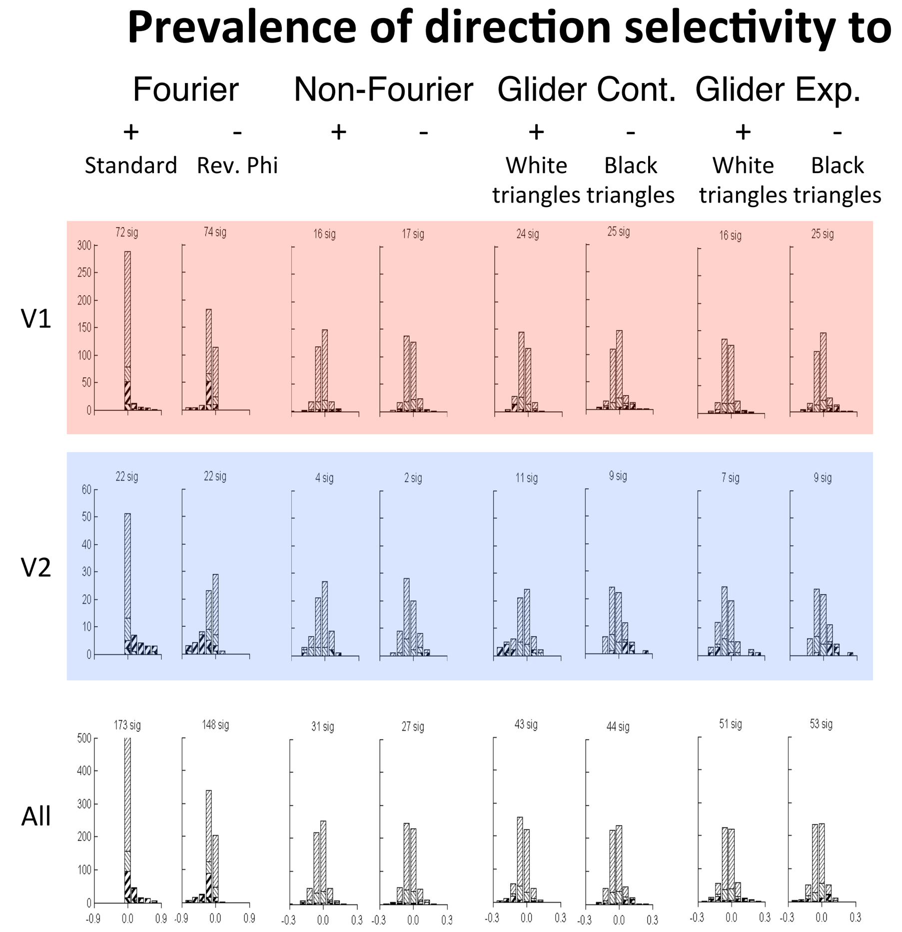
$$MC = \underbrace{|0.59+(-0.62)|}_{0.03} + \underbrace{|0.05+(-0.01)|}_{0.04} + \underbrace{|(-0.11)+0.13|}_{0.02} + \underbrace{|(-0.07)+0.04|}_{0.03} = 0.12$$

Example

Experiment name	DI	p-value
Fourier positive correlations	0 59	<0.001
Fourier negative correlations	-0.62	<0.001
NF positive correlations	0.05	0.091
NF negative correlations	-0.01	0.683
Glider Cont. white triangles	-0.11	<0.001
Glider Cont. black triangles	0.13	<0.001
Glider Exp. white triangles	-0.07	0.001
Glider Exp. black triangles	0.04	0.055

This table quantifies the motion responses of the neuron in the top row, right above. Consistent with an opponent mechanism, the DI values for positively correlated Fourier motion (standard motion) and negatively correlated Fourier motion ("reverse phi") are equal and opposite. There is also a modest but highly significant DI for glider contraction with white triangles.

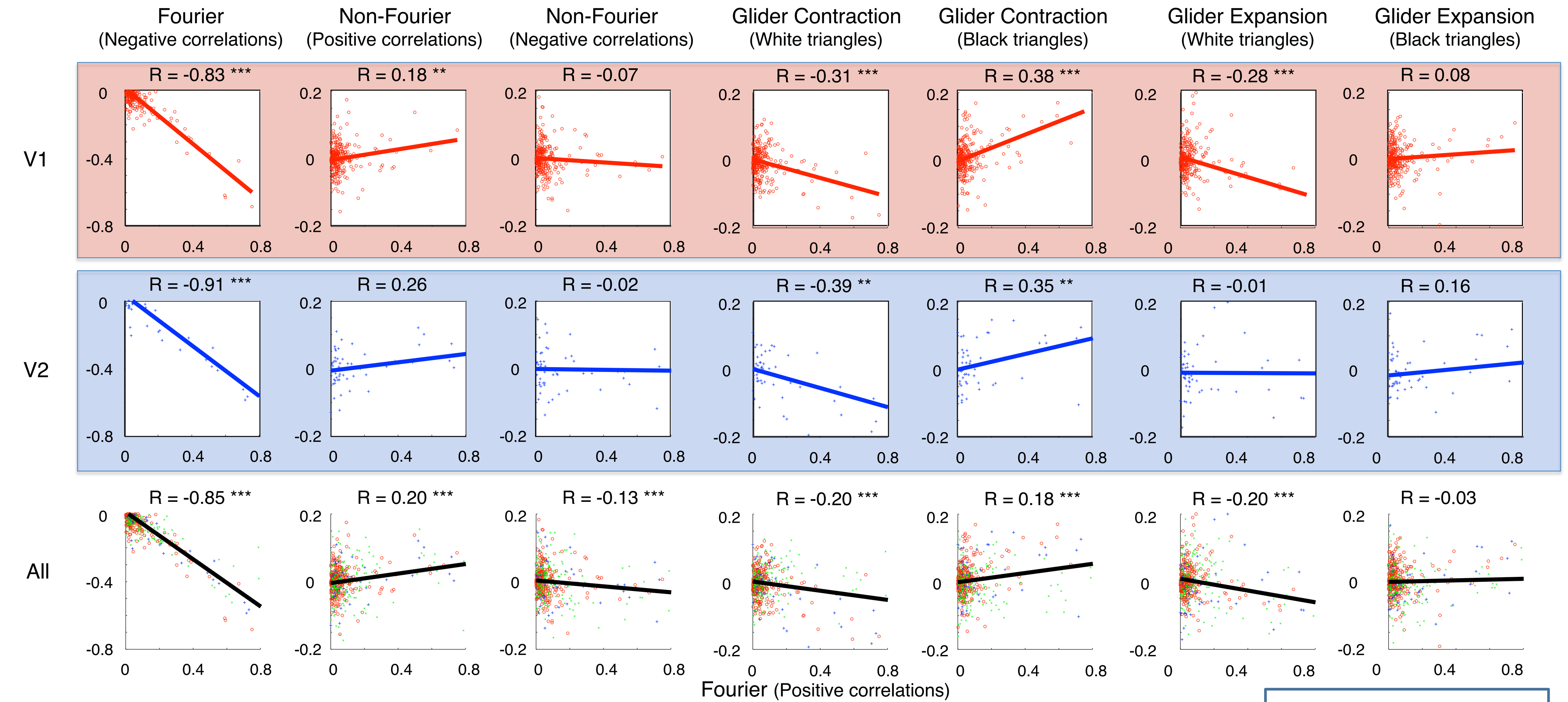
Prevalence of direction selectivity to F, NF and G motions



Each histogram shows the distribution of DI values for the several motion types analyzed. Note that we arbitrarily assigned "left" and "right" directions for the stimuli so that the DI for each neuron's response to Fourier motion was positive. All other DI values, therefore, reflect directional selectivity as referenced to the preferred direction for Fourier motion. For example, nearly all neurons had a selectivity for reversed-phi motion (second column) that was opposite to their selectivity for standard Fourier motion (first column). DI for standard Fourier and Glider white triangle motions are also typically opposite.

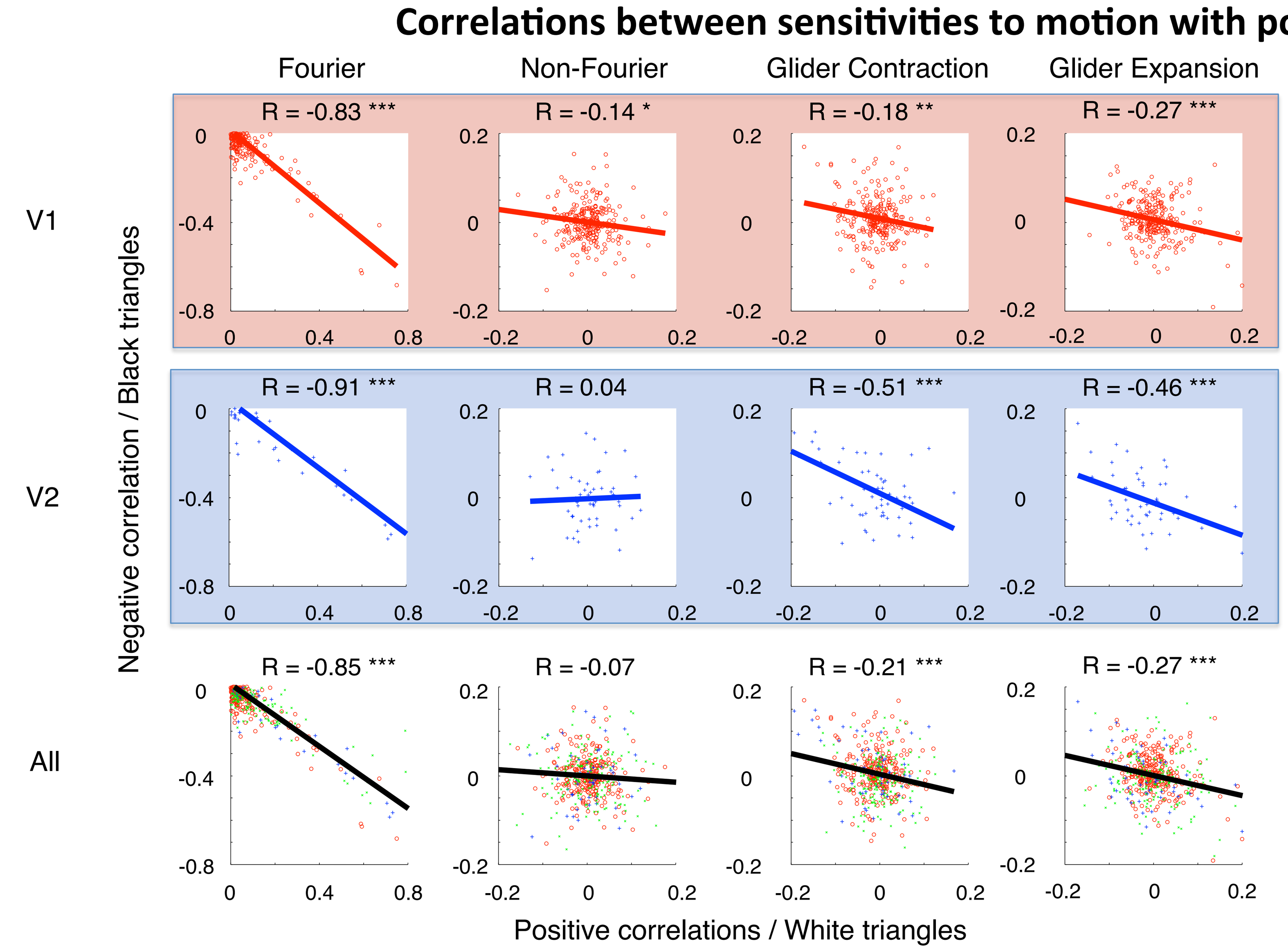
DI/Unit	Single	Multi
$P \le 0.05$		
$P > 0.05$		

Correlations between sensitivities of neurons to standard Fourier motion and other motion kinds



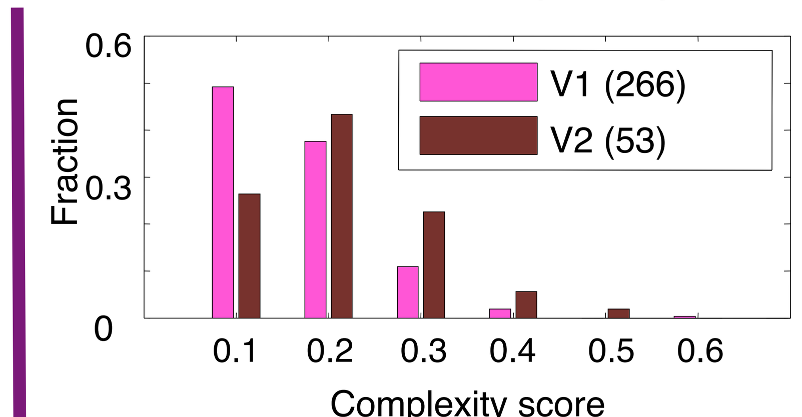
In each scattergram, the abscissa is the DI for standard F; the ordinate is the DI for one of the other motion types. There is a very strong negative correlation for reversed-phi motion (first column), and weaker but highly significant positive and negative correlations for most of the other motion types. Findings in V1 and V2 are similar. The R values are Pearson correlation; * indicates p<0.05, ** indicates p<0.01 and *** indicates p <0.001. Note difference in ordinate scale between first column and subsequent ones. Only neurons that were clearly identified as "single units" were included in this analysis.

Correlations between sensitivities to motion with positive and negative correlations



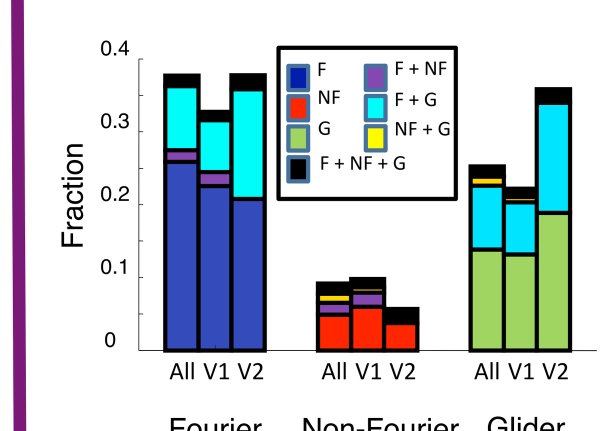
In the standard Hassenstein-Reichardt (HR) model (Reichardt 1961) for detection of F motion, correlations are calculated by products of contrast values, and correlations in opposing directions are compared. Neurons that embody this "opponent" model should therefore have opposite DI's for motion stimuli with positive correlations, vs. stimuli with negative correlations. These scattergrams show that this holds well as an approximation for F motion, and to a weaker extent for NF and G motion. The R values are Pearson correlation; * indicates p<0.05, ** indicates p<0.01 and *** indicates p <0.001. Only neurons that were clearly identified as "single units" were included in this analysis. Note difference in scales between first column and subsequent ones.

Motion complexity

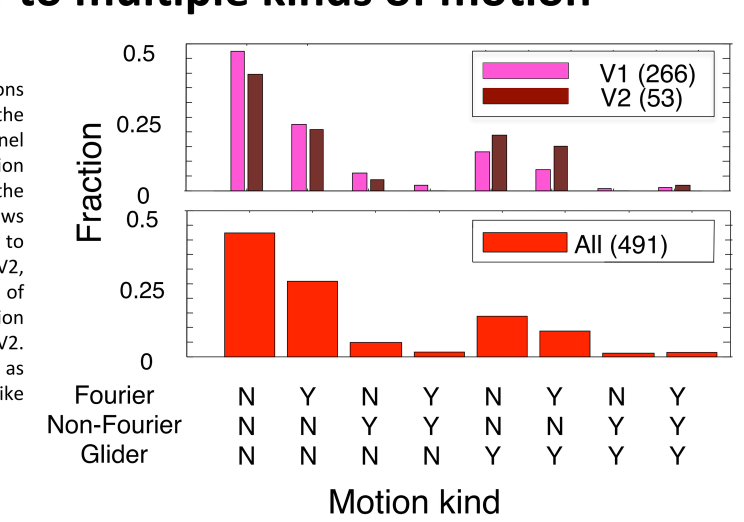


The motion complexity (MC) score (see middle panel for definition) indicates whether responses are consistent with a generalized opponent motion model (MC=0) or not (MC>0). MC scores were higher in V2 than in V1 (median in V2, 0.14; in V1, 0.10; KS test, p < 0.001). Only neurons that were clearly identified as "single units" were included in this analysis.

Prevalence of direction sensitivity to multiple kinds of motion



These panels show the prevalence of neurons with significant DI's for combinations of the three main kinds of motions. The left panel shows, for neurons responsive to each motion type, the fraction that is also responsive to the other types of motion. The right panel shows the fraction of neurons that are responsive to given combinations of motion. In V1 and V2, the pattern of responses to multiple kinds of motion is similar, but there is a greater fraction of neurons with sensitivity to G motion in V2. Only neurons that were clearly identified as "single units", based on amplitude and spike shapes, were included in this analysis.



Summary

- Neurons in macaque V1 and V2 respond to Fourier, non-Fourier, and glider motions.
- The prevalence of motion sensitivities is similar across areas.
- Individual neurons' responses to the different motion types are partially correlated.
- Complexity of motion computation was summarized by an index of consistency with opponent processes. This showed increased complexity in V2 compared to V1.

References

Chubb C, Sperling G (1988) Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. J Optical Soc Am A 5:1986 –2006.
Hu Q, Victor JD, (2010) A set of high-order spatiotemporal stimuli that elicit motion and reverse-phi percepts. J Vis. 10(3):9.1-16.
Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. Sensory communication, 303–317.
Nitzany EI, Victor JD. (2012). What kinds of local motion signals are present in naturalistic movies? Cosyne Abstract 2012, Salt Lake City USA.
Hazan, L., Zugaro, M., & Buzsáki, G. (2006). Klusters, NeuroScope, NDManager: a free software suite for neurophysiological data processing and visualization. Journal of neuroscience methods, 155(2), 207-216.

Supported by EY7977, EY9314 . E.I.N is also supported by the Tri-Institutional Training Program in Computational Biology and Medicine.