Independent and Redundant Information in V1: Different Stimulus Types

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Do nearby neurons transmit redundant information?
Does it matter which neuron fires which spike?
How do information rates depend on stimulus type?

METHODS

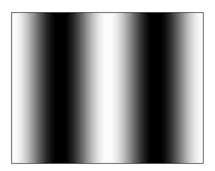
Physiology

- macaque V1, sufentanil anesthesia
- tetrode recordings of well-isolated nearby neurons

Stimuli

- stimuli presented at 5 contrasts (1/16, 1/8, 1/4, 1/2, 1)

M-Sequences
- luminance of each check modulated by same m-sequence
- pattern updated every 14.8 msec
- total duration: 60.6 sec or 7.6 sec
- optimal orientation



Stationary Sinusoidal Gratings
- optimal spatial frequency, orientation, spatial phase
- flashed on for 237 msec
- response measured between 30 and 300 msec after onset

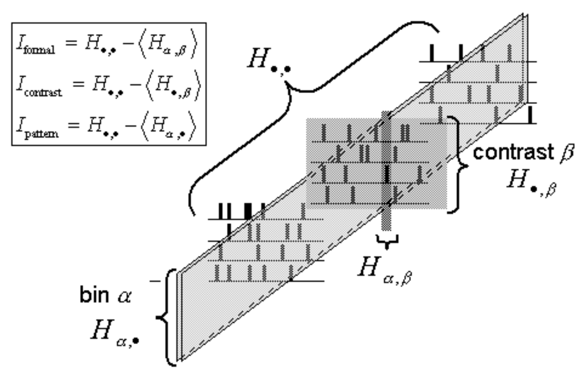
Drifting Sinusoidal Gratings
- optimal spatial frequency, orientation, temporal frequency

"Direct" Information Calculation (from Strong et al. 1998)

- *intuition*: response variability (entropy) not related to intrinsic noise must be stimulus-related
- information: [entropy across time] - [entropy across trials]
- entropy is calculated from spike counts in each response time bin
- normalize information by bin width to get *typical information rate* (bits/s)
- not enough data to consider correlations between time bins

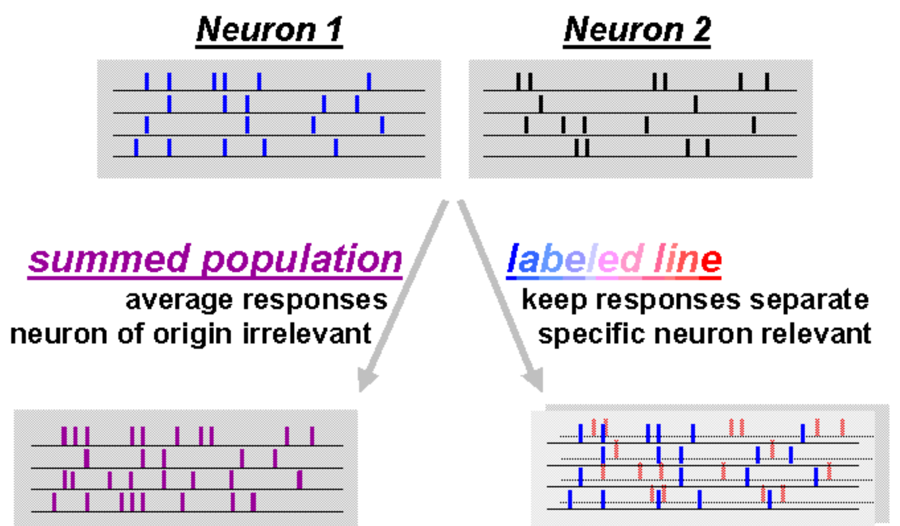
Extension to Stimulus Attributes

- ***formal***: typical overall stimulus-related information rate
- ***attribute-specific***: typical rate at which information about a particular stimulus attribute (contrast or spatiotemporal pattern) is transmitted
- ***confounded***: [formal info. rate] - Σ [attribute-specific info. rates]



Extension to Multiple Neurons

- two codes are examined

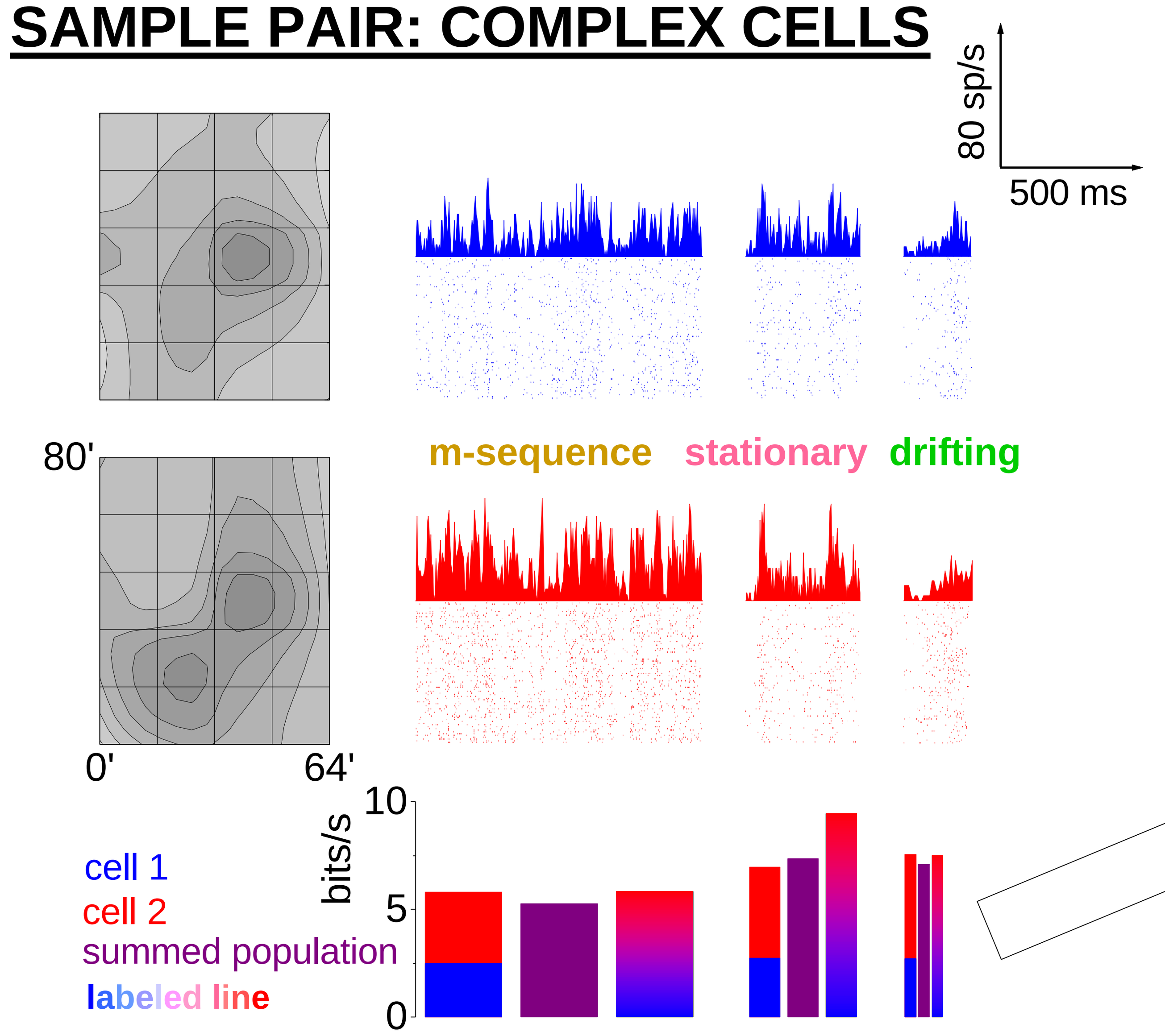


- for labeled line code, each time bin contains a vector of spike counts (each dimension corresponds to a different neuron)
- labeled line code captures all the information in the short-time limit
- summed population code cannot transmit more information
- analysis reveals the amount of information contained in the identity of the neuron that fires each spike

Bias Correction

- accurate information calculation requires infinite amounts of data
- an analytic correction exists for limited data (Miller, 1955; Treves and Panzeri, 1995)
- no analytic correction can offset large bias that results from time bins with few spikes
- *empiric correction:* across consecutive time bins with few spikes (low firing rates), assume that entropy changes slowly
- such bins can then be grouped together for purpose of estimating entropy
- procedure is validated on synthetic (inhomogeneous Poisson) spike trains

SAMPLE PAIR: COMPLEX CELLS

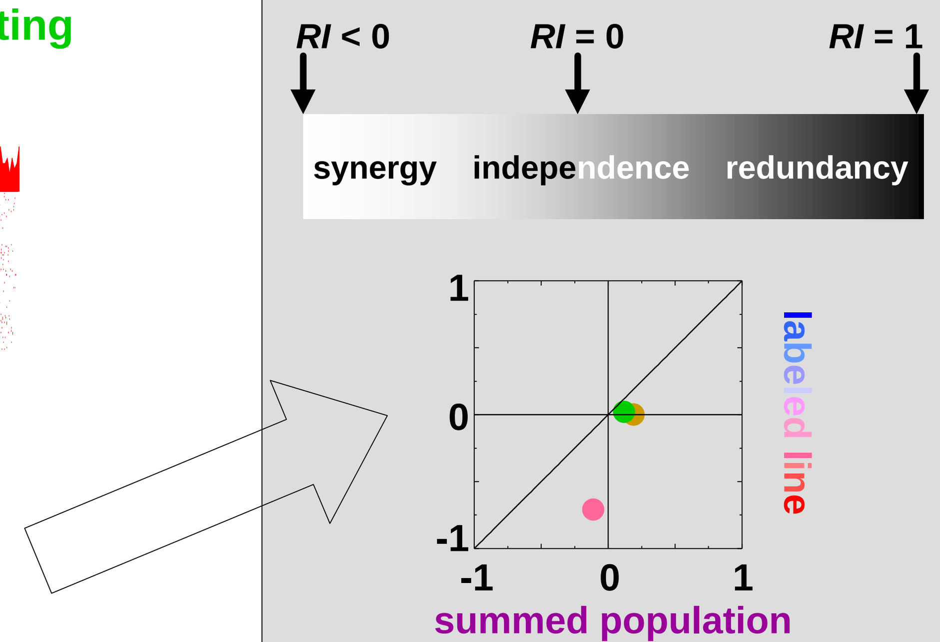


- Cells have similar and overlapping receptive fields, similar firing rates, and similar information rates.
- Averaging responses across neurons (summed-population code) leads to small decrease in information rate for m-sequence and drifting-grating responses, but small increase for stationary-grating response.
- For this pair of neurons, paying attention to neuron that fires each spike (labeled-line code) does not make a big difference (information rate is only slightly higher).
- In response to stationary gratings, the neurons transmit information synergistically (labeled-line information rate > Σ individual information rates).

Redundancy Index

$$RI = \left(1 - \frac{I_C}{I_{SS}}\right) \Big/ \left(1 - \frac{1}{N}\right)$$

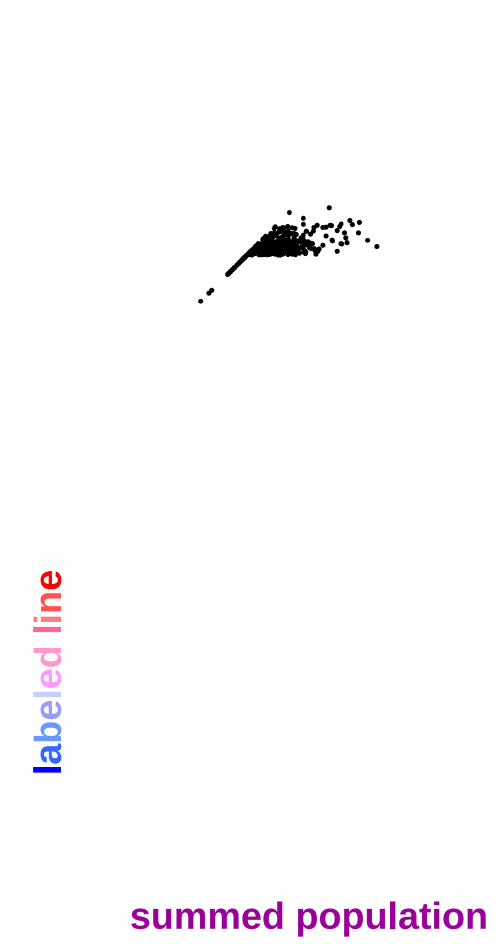
- I_C info. rate in summed population or labeled line code
- I_{SS} sum of info. rates for each neuron
- N # neurons



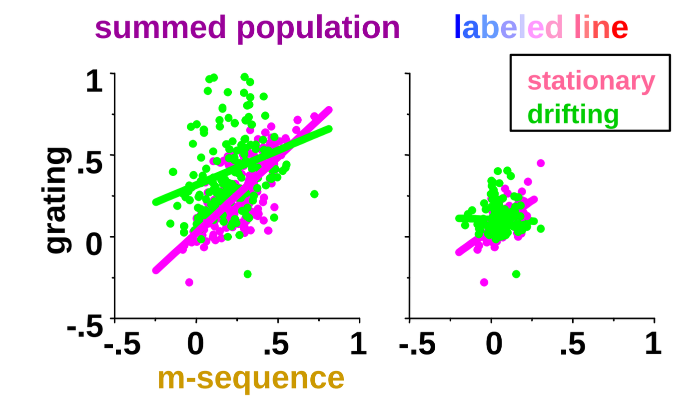
- Redundancy index is a measure of the degree to which different neurons transmit similar information.
- Information can be redundant for both summed-population and labeled-line codes.
- Synergy in stationary-grating responses is substantially more pronounced with labeled-line code.

POPULATION SUMMARY: *Redundancy Indices*

Effect of Multi-Neuron Code



Effect of Stimulus Type



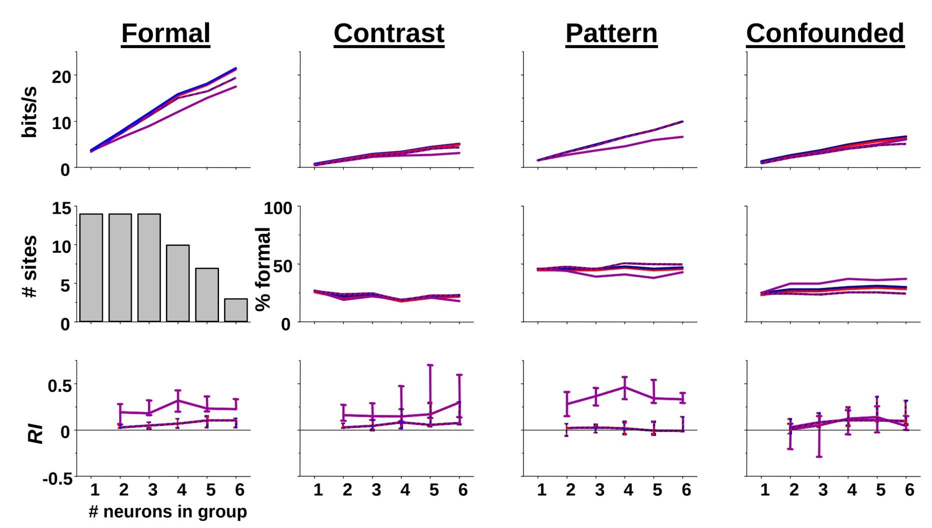
- Labeled-line *RI*'s are much more tightly clustered (similar) than summed-population *RI*'s.
- *RI*'s are correlated for responses to different stimulus types (here, m-sequence vs. stationary and drifting gratings).
- This indicates that independent information transmission is more a property of the neurons in the group than of the particular type of stimulus.

Results
- Information transmission across nearby neurons is generally independent (*RI*'s slightly positive but close to 0 overall).
- Independence is noticeably greater (*RI* closer to 0) for labeled line code (pay attention to which neuron fires which spike) than for summed population code (average responses across neurons).
- Synergy (*RI*<0) and redundancy (*RI*=1) are rare, as are situations in which additional neurons degrade the rate of transmitted information (*RI*>1).

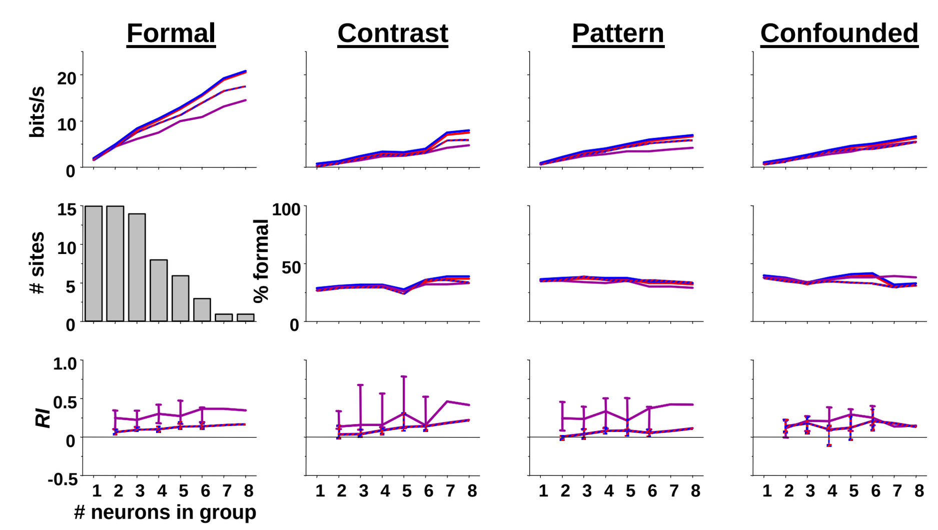
Notes
- Data from different stimulus types and group/cluster sizes are included.
- Formal redundancy indices include data from responses to stationary gratings presented at a variety of contrasts, spatial phases, spatial frequencies, and orientations.
- Open circles show median values (separately calculated for each code).

POPULATION SUMMARY: *Attribute-Specific Information Rates*

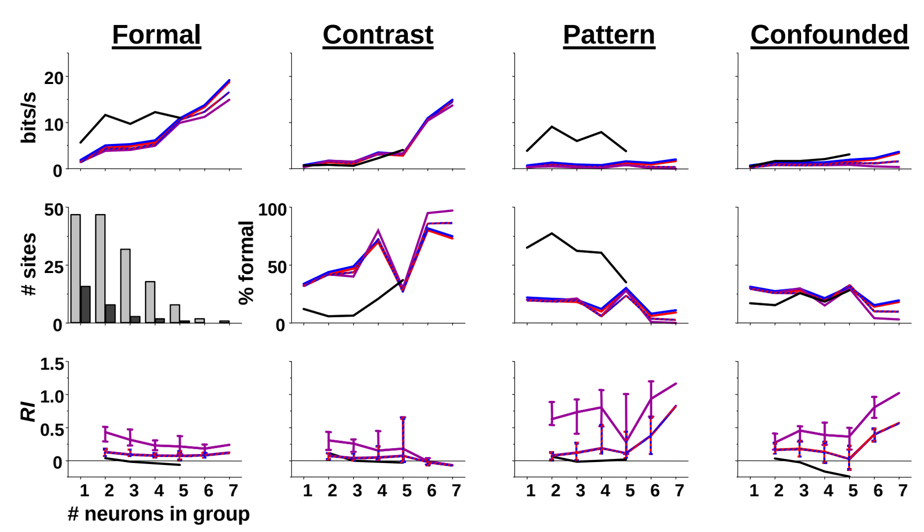
M-Sequences



Stationary Gratings



Drifting Gratings



error bars on *redundancy indices* come from 200 bootstrap resamplings

- Values plotted are *medians* across recording sites (separate medians calculated at each site).
- Histograms show # of sites at which groups of each size were recorded (cumulative distributions).
- *Formal* (overall) and *pattern*-specific information: averaging across neurons (summed-population code) leads to progressively larger loss of information vs. paying attention to neuron that fires each spike (labeled-line code).
- This is reflected in the *redundancy indices*, which are near 0 for the labeled-line code but more positive for the summed-population code.
- *Contrast-related* information: virtually no information loss from averaging across neurons.
- Information confounded between *contrast* and *spatiotemporal pattern* is about 25% of the total, regardless of # of neurons.
- Simple cells transmit much more pattern-related information in response to drifting gratings (solid lines).

OBSERVATIONS

- Nearby neurons in V1 convey nearly independent stimulus-related information.
- *Formal and spatiotemporal pattern*-specific information is significantly more independent if both the times of spikes and their neurons of origin are considered, rather than the spike times alone (median *RI* for *formal* information: 0.062 vs. 0.27, respectively). In other words, the identity of the neuron that fires each spike conveys information.
- *Contrast*-specific information is also conveyed independently by nearby neurons, but the neuron of origin matters much less.
- Thus, the simplest, most reliable way for the visual system to estimate the *contrast* of a visual scene would be to average responses over a local cluster of neurons. This type of averaging would fail if *spatiotemporal pattern*-related information were to be extracted.
- The amount of *confounded* information (information not specifically attributable to *contrast* or *spatiotemporal pattern*) grows in proportion to the number of neurons in the pool, regardless of the type of code. *Confounded* information is also independently transmitted by nearby neurons.

NOTES

- Information rates are calculated in the short-time limit, so we don't consider correlations in stimuli or responses. Accounting for such correlations would require longer, multi-letter words, but accurate information estimates from such words demand enormous amounts of data. Correlations are likely to lower information rates, more so for stationary- and drifting-grating responses than for m-sequence responses.
- Information rates are not additive over time.
- *Confounded* information arises from the effects of spatiotemporal pattern on the dynamics of contrast encoding, and vice versa. Mechanisms for this interaction include contrast gain control and normalization.

MORE INFORMATION

- http://westside.med.cornell.edu
- reichd@rockefeller.edu
- Reich, DS; Mechler F; Victor JD (2001). Formal and attribute-specific information in primary visual cortex. *J Neurophysiol* **85**(1): 305-318. *(Covers single-unit responses only.)*