Adaptation of intrinsic circuit correlations and synergy in retinal synchrony

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OVERVIEW

Recent work predicts that population-level adaptation should occur in response to stimulus variations [1]. We test this prediction using simultaneous recordings from populations of retinal ganglion cells [2] and a new extension to the maximum entropy framework, time-dependent maximum entropy (TDME) [3].

We find that:

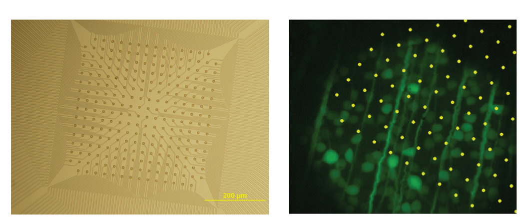
- network interactions change during natural stimulus presentation
- adaptation shapes the relationship between synergy and redundancy while maintaining fixed information per pattern
- adaptation effects are stronger in more synchronous patterns where many neurons fire simultaneously

Our results suggest that adaptation occurs not only on the single-neuron level, but also on the population level, to adapt the vocabulary of activity patterns in response to stimulus variations.

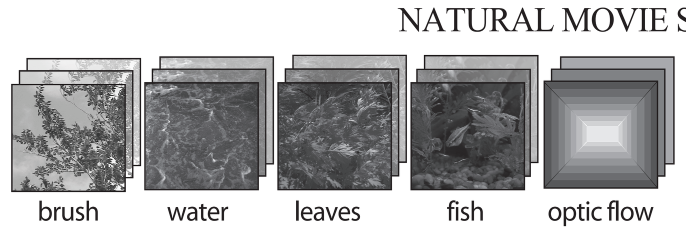
EXPERIMENTAL METHODS

RETINAL RECORDINGS

- recordings were performed on tiger salamander retinae using a rectangular 252 multi-electrode array with 30μm spacing and 10kHz sampling rate per channel [2]
- waveforms were sorted using custom spike-sorting algorithms (10 well-sorted cells were selected for the subsequent analyses presented here)



NATURAL MOVIE STIMULI



- five randomly interleaved natural movies representing a variety of natural conditions
- each movie lasted a total duration of 20s and was repeated 80-90 times

TIME-DEPENDENT MAXENT MODEL

Time-dependent maximum entropy (TDME) can separate true network interactions from stimulus-induced apparent interactions

spike trains $\sigma_i(t)$ are discretized into time bins of width $\Delta t = 20$ms

$$\sigma_i(t) = \begin{cases} 1 & \text{neuron } i \text{ fired in time bin } t \\ 0 & \text{neuron } i \text{ was silent in time bin } t \end{cases}$$

the joint probability of binary firing patterns $P\{\vec{\sigma}\}$ is well-approximated by:

$$P(\{\vec{\sigma}\}\,|\,t) = \frac{1}{Z(\{h_i^s, h_i(t), J_{ij}\})} \exp\left[\sum_i \left(h_i^s + h_i(t)\right)\sigma_i + \frac{1}{2}\sum_{i,j} J_{ij}\sigma_i\sigma_j\right]$$

model parameters are chosen to exactly reproduce observables of data

model parameters:		observables:	
h_i^s	intrinsic bias to fire	$\langle\sigma_i\rangle$	average firing rate
$h_i(t)$	time-dependent bias to fire	$\langle\sigma_i(t)\rangle$	time-dependent firing rate
J_{ij}	effective functional coupling	$\langle\sigma_i\sigma_j\rangle$	covariance in spike trains

we compute the information that $\{\vec{\sigma}\}$ encodes about the stimulus

information conveyed by a single pattern $\vec{\sigma}$ at time t:

$$I_{\vec{\sigma}}(t) = \frac{P(\vec{\sigma}|t)}{P(\vec{\sigma})}\log_2\left(\frac{P(\vec{\sigma}|t)}{P(\vec{\sigma})}\right)$$

information conveyed by the ensemble of patterns $\{\vec{\sigma}\}$ over the stimulus duration:

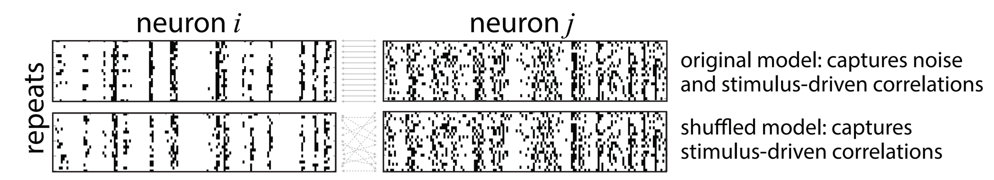
$$I(\{\vec{\sigma}\};t) = \sum_{\{\vec{\sigma}\}} P(\vec{\sigma})\,\frac{1}{T}\int_0^T dt\; I_{\vec{\sigma}}(t)$$

With TDME, one can approximate the information $I(\{\vec{\sigma}\};t)$ that the entire population carries about the stimulus

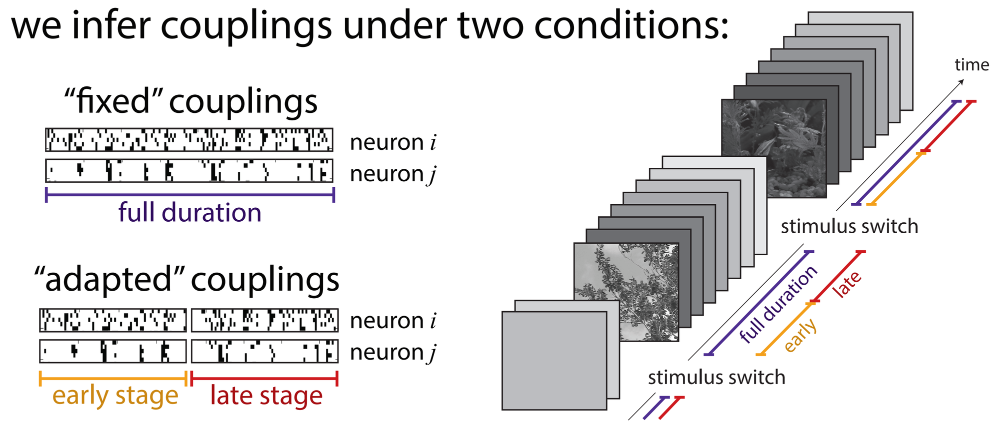
NETWORK INTERACTIONS ADAPT DURING STIMULUS PRESENTATION

MODEL CONSTRUCTIONS

to check that TDME separates stimulus-driven from intrinsic network interactions, we compare models inferred with and without repeat shuffling:



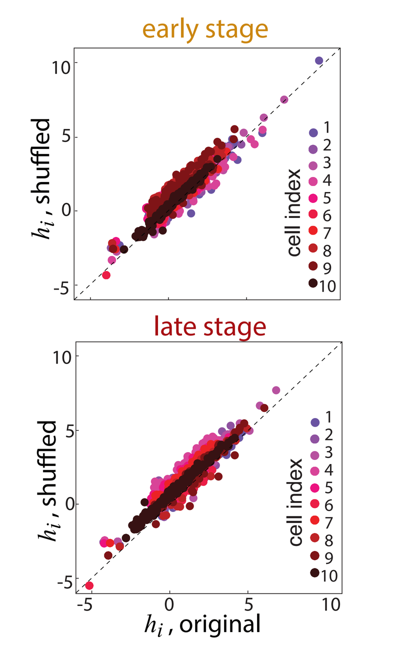
to examine adaptation during stimulus presentation, we infer couplings under two conditions:



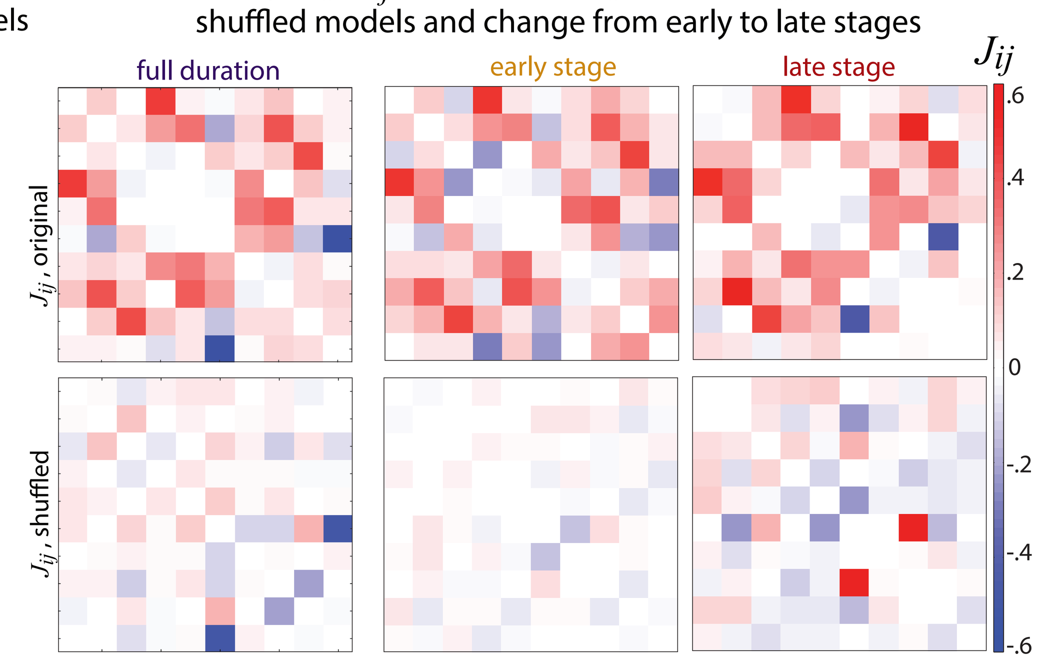
MODEL COMPARISONS

single-cell biases to fire (h_i) largely capture stimulus-driven correlations, while couplings (J_{ij}) largely capture intrinsic circuit correlations

a). biases to fire h_i are highly-correlated between models



b). couplings J_{ij} are much stronger in the original versus shuffled models and change from early to late stages



ADAPTATION SHAPES SYNERGY IN SYNCHRONY

SYNERGY IN COMPOUND PATTERNS

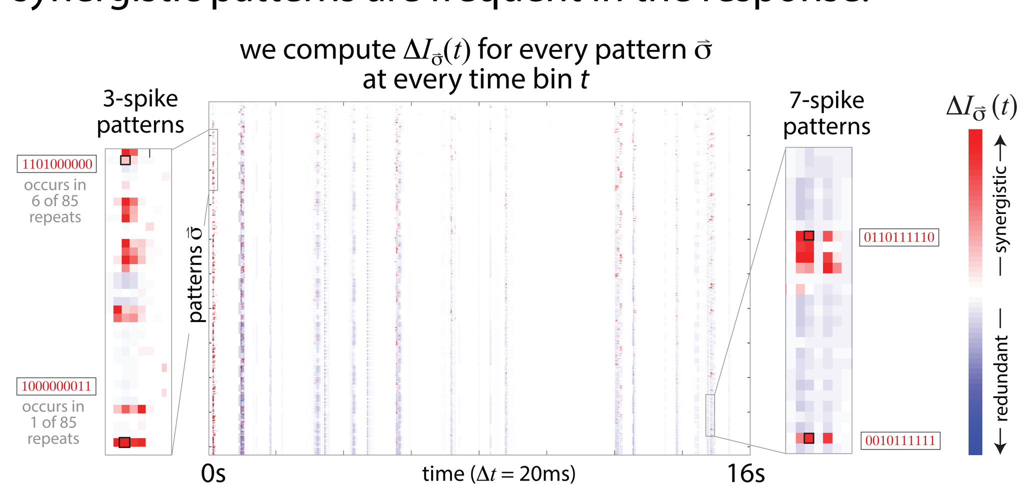
we identify synergistic and redundant occurrences of a compound pattern $\vec{\sigma}$ by computing $\Delta I_{\vec{\sigma}}(t)$ [4]:

$$\Delta I_{\vec{\sigma}}(t) = I_{\vec{\sigma}}(t) - \sum_i I_{\sigma_i}(t) \quad \begin{cases} < 0 & \text{redundant occurrence at } t \\ > 0 & \text{synergistic occurrence at } t \end{cases}$$

e.g. $\vec{\sigma} = [1011000000]$:

$$\Delta I_{\vec{\sigma}}(t) = \underbrace{I_{\vec{\sigma}=[101\ldots0]}(t)}_{\text{information conveyed by pattern as a whole}} - \underbrace{[\,I_{\sigma_1=1}(t) + I_{\sigma_2=0}(t) \ldots + I_{\sigma_{10}=0}(t)\,]}_{\text{sum of information values conveyed by individual pattern components}}$$

synergistic patterns are frequent in the response:



synergistic patterns account for a large fraction of information:

$$f_{syn} = \underbrace{\sum_{\{\vec{\sigma}\}} P(\vec{\sigma})\,\frac{1}{T}\int_0^T dt\; I_{\vec{\sigma}}(t \text{ where } \Delta I_{\vec{\sigma}} > 0)}_{I_{syn}(\{\vec{\sigma}\};t)} \Big/ \underbrace{\sum_{\{\vec{\sigma}\}} P(\vec{\sigma})\,\frac{1}{T}\int_0^T dt\; I_{\vec{\sigma}}(t)}_{I(\{\vec{\sigma}\};t)}$$

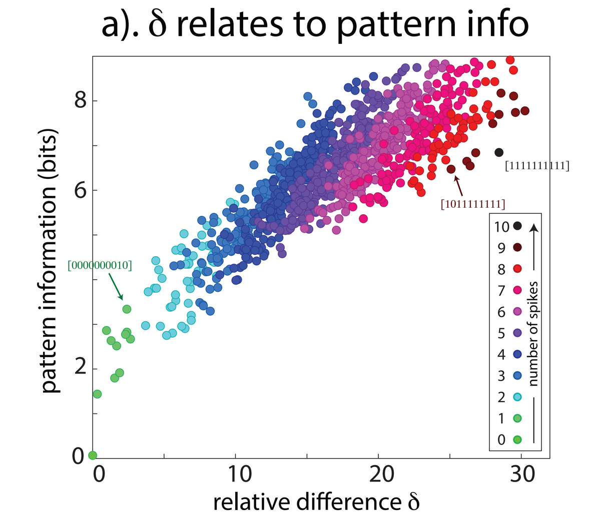
	natural movie stimuli				
	brush	water	leaves	fish	flow
I_{syn} (bits)	.196	.0498	.255	.267	.468
I (bits)	.321	.112	.399	.372	.649
$f_{syn} = I_{syn}/I$	.611	.444	.640	.718	.722

SYNERGY, REDUNDANCY, AND PATTERN INFORMATION

adaptation shapes the relative difference $\delta_{\vec{\sigma}} = S_{\vec{\sigma}} - R_{\vec{\sigma}}$ between synergistic ($S_{\vec{\sigma}}$) and redundant ($R_{\vec{\sigma}}$) occurrences of each pattern $\vec{\sigma}$:

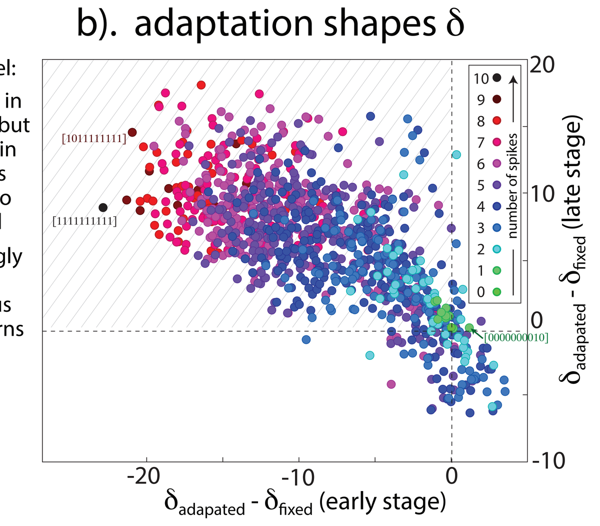
$$\delta_{\vec{\sigma}} = \left[\frac{1}{T}\int_0^T dt\,(\Delta I_{\vec{\sigma}}(t) > 0)\right] - \left[\frac{1}{T}\int_0^T dt\,(\Delta I_{\vec{\sigma}}(t) < 0)\right] = S_{\vec{\sigma}} - R_{\vec{\sigma}}$$

a). δ relates to pattern info

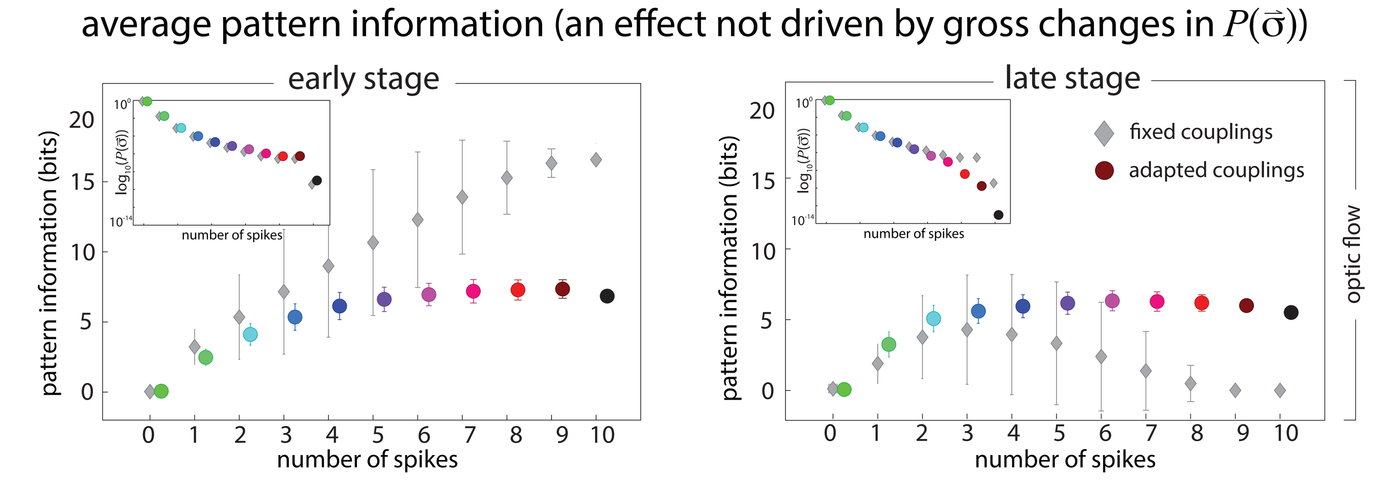


b). adaptation shapes δ

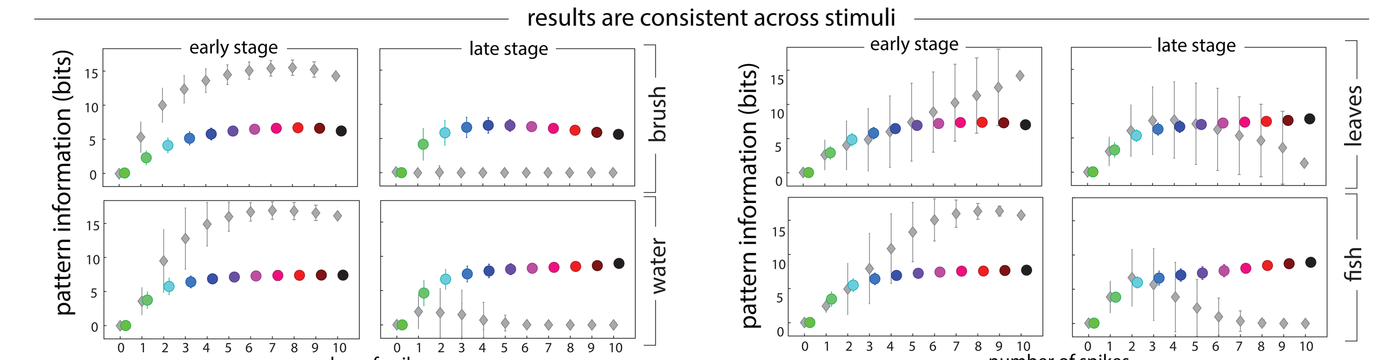
adapted model:
- decreases δ in early stage but increases δ in late stage as compared to fixed model
- more strongly shapes δ in synchronous firing patterns



c). adaptation-driven changes in δ have the effect of maintaining a fixed average pattern information (an effect not driven by gross changes in $P(\vec{\sigma})$)



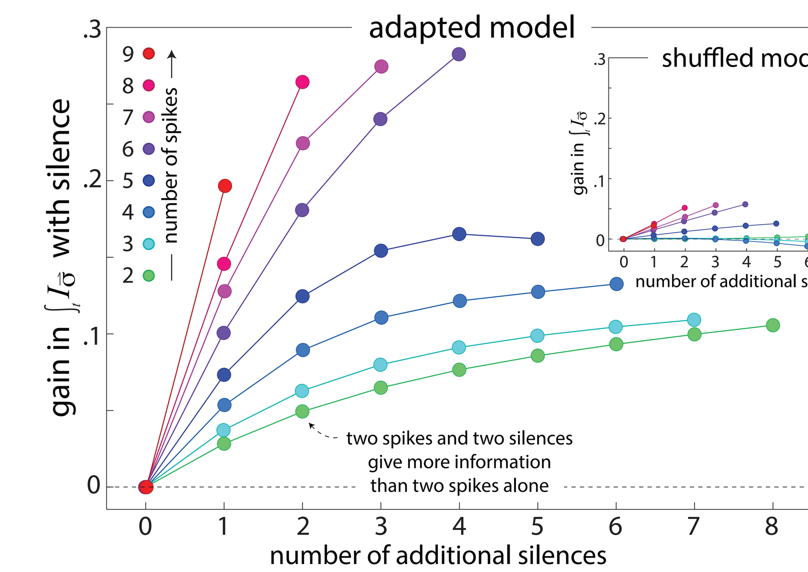
results are consistent across stimuli



OUTLOOK

INFORMATION IN SILENCE

network interactions increase symbol information in silence [4]:



e.g. gain in $\int_t I_{\vec{\sigma}}$ with silence for two-spike pattern $\vec{\sigma}$ = [11]:

1 silence	2 silences	3 silences	…	8 silences
$I([110])-I([11])$	$I([1100])-I([11])$	$I([11000])-I([11])$	…	$I([1100000000])-I([11])$

- synchronous patterns are more informative in the presence of silent cells
- the gain in infomation increases more rapidly for more synchronous symbols
- the shuffled model (in which circuit correlations are destroyed; inset) does not capture this effect
- this suggests that network-level adaptation shapes information in silence and plays an increasingly important role as population sizes increase

network adaptation might increase information per nonsilence at a population level:

		natural movie stimuli				
		brush	water	leaves	fish	flow
info/nonsilence (bits) $\frac{I(\{\vec{\sigma}\};t)}{1-P([0000000000])}$	early (shuffled)	2.59 (2.61)	1.90 (1.91)	2.41 (2.40)	3.15 (3.13)	2.99 (2.99)
	late (shuffled)	2.19 (2.20)	1.39 (1.47)	2.76 (2.75)	4.39 (4.35)	3.27 (3.22)
	late - early	-.42	-.52	+.34	+1.24	+.28

SUMMARY

We use a new approach (TDME) to construct the time-dependent distribution of activity patterns in neural populations. This approach enables us to identify the information content of synergistic patterns:

we find that synergistic patterns contribute a significant fraction of the information conveyed by the population

Within this framework, we developed a method for isolating the role of network interactions in shaping population activity:

we find that network adaptation shapes the relationship between the synergy and redundancy of synchronous firing patterns while maintaining fixed average information per pattern

Preliminary results suggest an important role for population silence:

network interactions increase the information of synchronous patterns in the presence silence and could increase information per nonsilence

Together, these results suggest that network adaptation shapes population-level activity in response to stimulus variations

ACKNOWLEDGEMENTS

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