Spike train analysis reveals cooperation between Area 17 neuron pairs that enhances fine discrimination of orientation.

J. M. Samonds[1], J. D. Allison[2], H. A. Brown[1], and A. B. Bonds[1,2], Departments of Biomedical Engineering[1] and Electrical Engineering and Computer Science[2], Vanderbilt University, Nashville, TN 37235.

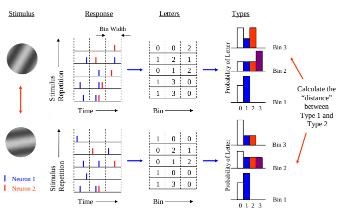
PURPOSE

Bursting in Area 17 is tuned more sharply than spike rate for orientation (OR) and spatial frequency (SF) (Cattaneo et al., 1981a,b). Burst length is reduced at non-optimal orientations (DeBusk et al., 1997) and leads to less efficient synaptic coupling (Snider et al., 1998). We describe how these interspike interval (ISI) properties could contribute to discriminations between spike trains for fine and gross differences in OR and SF. We also describe changes in neural dependency as a function of OR, SF, contrast, and time to demonstrate how cooperative information (synergy) arises and is transmitted.

METHODS

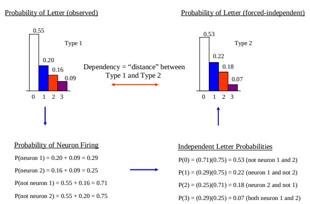
We recorded from 22 pairs of neurons neurons in cats anesthetized with Propofol and N_2O and paralyzed with Pavulon following established guidelines. We used type analysis (Johnson et al., 2001) to calculate the Resistor Average Kullback-Leibler distance between ensemble responses to fine (<10deg, <0.1c/deg) and gross (>10deg, >0.1c/deg) variations of OR and SF from the optimal parameter (see panel below). This "distance" provides an estimate of the reduction in classification error between responses (i.e., reduction in error = $2^{-\text{distance}}$). Discharge history was incorporated into types by testing for a stable Markov order (i.e., where discharge history ceases to contribute) using conditional types on previous bins for distance calculations.

Calculation of Types (Probability Mass Functions)

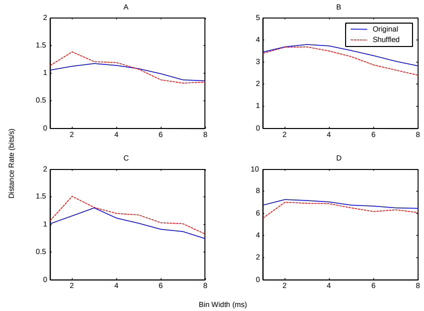


We measured the connectivity between neurons with a dependency distance. Dependency is the distance between the type of the original response and a type formed under the assumption the neurons are independent (forced-independent; see panel below). We tested this method with variations of OR, SF, and contrast to examine the temporal dynamics and tuning of dependency for each stimulus property. We used the bin width that produces the greatest distance to estimate the lag time or precision of the connectivity.

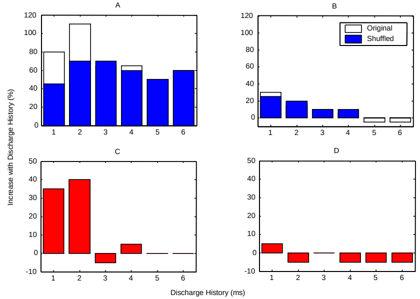
Transneural Correlation



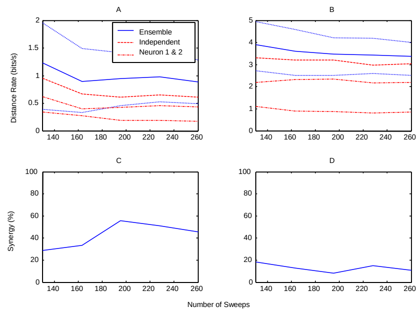
TEMPORAL RESOLUTION



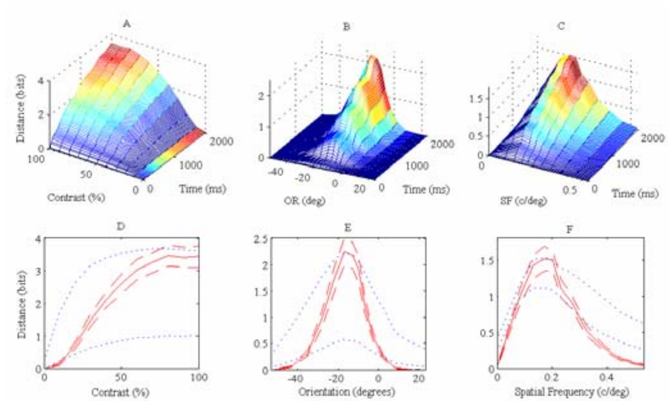
DISCHARGE HISTORY



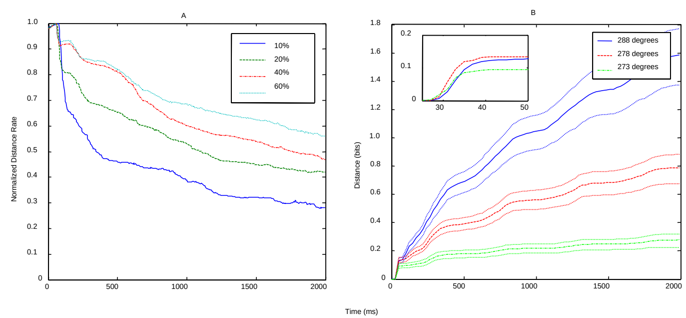
SYNERGY ESTIMATIONS



DEPENDENCY TUNING



TEMPORAL DYNAMICS



ABOVE: **(1) Dependency Tuning:** We measured dependency (connectivity) across (A) contrast (2-ms bins), (B) OR (2-ms bins), and (C) SF (3-ms bins) across the 2-second stimulus duration to produce a mesh. The accumulated dependency (at 2 seconds) between the neurons was lower than expected (rate response in blue) for (D) contrast modulations. The dependency tuning was narrower than rate tuning (blue) for (E) OR (narrower than even burst tuning) and (F) SF. **(2) Temporal Dynamics:** (A) To examine the adaptation that lead to the lower than expected dependency, the dependency for contrast was converted to a distance rate and normalized by the initial dependency rate. We found that adaptation was faster for lower contrasts. (B) The narrow tuning of dependency only becomes apparent after the initial step at 30-45 ms (see inset >8 bits/s) when the rates at 278 and 273 degrees are reduced much more drastically (<<1 bit/s) than the peak response (288 degrees; ~1 bit/s).

LEFT COLUMN: **(1) Temporal Resolution:** We varied the bin width of the types from 1-8 ms to show the variation in the distance rate for (A) fine and (B) gross differences in SF and (C) fine and (D) gross differences in OR. The original responses were shuffled to remove neural dependencies (connectivity) from possible independent ISI influences (bursts). **(2) Discharge History:** After we determined that the distance did not increase beyond a Markov order of 1 (1 bin of discharge history), we measured the percent increase in distance from a Markov order of 0 to 1 at bin widths of 1-6 ms for (A) fine and (B) gross differences in OR. When incorporating discharge history, dependent increases in distance (C and D) were separated from independent increases in distance (i.e., burst length) **(3) Synergy Estimations:** The ensemble distance (4-letter alphabet) is compared to the independent distance (sum of 2-letter types for neuron 1 & 2) for (A) fine and (B) gross differences in OR (same pair of neurons reported above). (C and D) The percent difference in (A and B). We compared the distance rates and synergy vs. random partial selections of stimulus repetitions to examine the confidence and precision of the distance and synergy estimates.

RESULTS SUMMARIZED

1) The peak temporal resolution of the distance rates (n = 12) was 2.3 ms (67.9% increase) for fine differences and 2.7 ms (29.5% increase) for gross differences after removing dependencies
2) Discharge history (2 ms) provided an average increase of 110% (n = 7, 55-250%) in distance for fine discrimination of OR (50% from dependencies), 70% (n = 4, 40-75%) increase for SF (20% from dependencies), and <20% for gross discriminations.
3) The average synergy for fine differences in OR was 50% (n = 7, 15-120%) , 25% (n = 4, 15-40%) for SF, and <10% for gross discriminations.
4) Narrow dependency (3.1 ms average bin width) tuning develops following a 15 ms delayed reduction in the initial strength for OR and SF.
5) Lower contrast leads to a faster decay in the dependency.
6) On average, dependency tuning was 42.5% (n = 9, 16.2-58.1%) narrower than rate tuning for OR and 29.2% (n = 5, 10.0-45.5%) narrower for SF.

CONCLUSIONS

1) The bin width at 2-5 ms serves as a low pass filter to enhance burst differences between optimal and non-optimal stimuli.
2) The discharge history enhances discrimination because burst length modulation and changes in synaptic efficiency occur between optimal and non-optimal stimuli.
3) The cooperation (synergy) between neurons is caused by continued changes in connectivity when the firing rate (and even burst rate) remains relatively constant.
4) The difference between dependency tuning and rate tuning is a result of the effect of bursts on synaptic efficiency. For OR, additional influences continue to modulate connectivity (i.e., burst length).
5) Contrast modulates isolated (non-burst) spikes (Cattaneo et al., 1981a,b) that raise the membrane potential (with chaos; Shadlen and Newsome, 1998) closer to threshold and reduce the integration time constant (Koch et al., 1996) so synchronization decays faster at lower contrast.
6) The narrow tuning of connectivity and the cooperation with only 2 neurons suggests that a coding scheme of synchronized assemblies (controlled by cortical mechanisms, i.e., intrinsic bursting and integrated chaos) could account for hyperacuity discriminations.

BIBLIOGRAPHY

Cattaneo A., Maffei L., and Morrone C. Patterns in the discharge of simple and complex visual cortical cells. *Proc. R. Soc. Lond.*, 212:279-297, 1981.

Cattaneo A., Maffei L., and Morrone C. Two firing patterns in the discharge of complex cells encoding different attributes of the visual stimulus. *Exp. Brain Res.*, 43:115-118, 1981.

DeBusk B. C., DeBruyn E. J., Snider R. K., Kabara J. F., and Bonds A. B. Stimulus-Dependent Modulation of Spike Burst Length in Cat Striate Cortical Cells. *J. Neurophysiol.*, 78: 199-213, 1997.

Johnson D. H., Gruner C. M., Baggerly K., and Seshagiri C. Information-Theoretic Analysis of Neural Coding. *J. Comp. Neurosci.*, 10:47-69, 2001.

Koch C., Rapp M., and Segev I. A brief history of time (constants). *Cereb. Cortex*, 6:93-101, 1996.

Shadlen M. N. and Newsome W. T. The Variable Discharge of Cortical Neurons: Implications for Connectivity, Computation, and Information Coding. *J. Neurosci.*, 18:3870-3896, 1998.

Snider R. K., Kabara J. F., Roig B. R., and Bonds A. B. Burst Firing and Modulation of Functional Connectivity in Cat Striate Cortex. *J. Neurophysiol.*, 80:730-744, 1998.