Would the same inferences about visual memory have been made with LFPs as compared to spikes?

Catrina M. Hacker¹, Simon Bohn¹, Brett L. Foster², Nicole C. Rust¹

¹ Department of Psychology, ² Department of Neurosurgery, University of Pennsylvania

Abstract

A central premise of basic neuroscience research is that insights about the healthy brain may eventually inform treatments for neurological and neuropsychiatric disorders. While much of the recent progress in systems neuroscience has relied on densely sampled, high spatial resolution measures of neural activity (like spikes), most neural recordings available in humans are field potentials. Consequently, bridging the divide between animal and human neuroscience requires understanding how neural representations compare in those different types of data. To fill this gap, we analyzed a dataset with established spiking representations of visual memory to answer a simple question: would the same inferences about the neural representations supporting memory have been made if measures were limited to field potentials? Using spike and local field potential (LFP) data simultaneously recorded in inferotemporal cortex (ITC) of four macaque monkeys performing a visual memory task, we show that the neural representations of three variables are aligned across spikes and high-gamma activity: memory, memorability, and contrast. In addition, we show that conditionspecific, and in some cases image-specific, neural representations are matched across both measures. These results suggest that data can be meaningfully compared across animals and humans in support of translational work, such as in developing brain computer interfaces and closed-loop therapeutic stimulation devices.

Keywords: LFPs; memory; memorability; repetition suppression; neural representations

Introduction

Over the last decade, technological advances have allowed systems neuroscience to make notable progress in understanding how neural activity drives behavior (Urai, Doiron, Leifer, & Churchland, 2022). Simultaneously, the field of human neuroscience has expanded, with researchers recording directly from the human brain to understand how it operates in health and disease (Jacobs & Kahana, 2010; Chang, 2015; Parvizi & Kastner, 2018). However, these two advances have largely relied on different types of neural signals, presenting a challenge to taking insights from one space to the other. In animals, insights most often rely on access to densely sampled, high spatial resolution measures of neural activity (spikes); in humans, most recordings, especially in therapeutic contexts, are field potentials. Thus, bridging the gap between animal and human neuroscience requires understanding how the nature of neural representations compares in spikes versus field potentials.

Previous studies have drawn connections between high gamma power (HG) in the LFP and spiking activity (Ray & Maunsell, 2011; Liu & Newsome, 2006; Kreiman et al., 2006) or HG and behavior (Henin et al., 2019; Sederberg et al., 2007), but largely failed to connect all three. This leaves open whether connections made in animal studies between spikes and behavior may be possible when e.g., recording from a human patient. In this study, we demonstrate that neural representations of visual memory are highly aligned in spikes and HG. Specifically, we show alignment for three variables known to influence spiking population response magnitude in inferotemporal cortex (ITC) to drive visual memory behavior: delay (Meyer & Rust, 2018), memorability (Jaegle et al., 2019), and image contrast (Mehrpour, Meyer, Simoncelli, & Rust, 2021). Excitingly, we also show that HG directly predicts memory behavior as well as spikes, suggesting that many insights about the neural representations that drive behavior from spikes may translate directly to human neuroscience, at least in the context of the magnitude coding schemes we analyze here.

Methods

Task

Neural data were recorded as four macaques (M1-M4) viewed a sequence of natural images and saccaded to a target to indicate whether each was novel or repeated. Images were randomly sampled from the internet (Meyer & Rust, 2018) and assigned memorability scores using MemNet (Khosla, Raju, Torralba, & Oliva, 2015). Each image appeared for 400 (M1/M2) or 500 (M3/M4) ms, followed by two choice targets. Images appeared exactly twice, once as novel and as repeated. The number of intervening images (n-back) was systematically varied. Two animals (M1/M2) also performed a variant of the task in which images appeared at either a high or low contrast (Mehrpour et al., 2021).

Neural Data

Wideband signals were recorded from ITC with a laminar 24channel U-probe. Neurons were identified by manually spike sorting offline. LFPs were extracted by low-pass filtering the voltage data to below 200 Hz and removing 60 Hz noise. Spectral information was extracted from the LFPs using Morlet wavelet decomposition and baseline subtracting the amplitude for each estimated frequency. High gamma was defined as the average amplitude in 50-150 Hz for a time window defined to match the spikes. Behavioral predictions were made by training a Fisher Linear Discriminant decoder to distinguish novel from repeated images based on reductions in firing rate. The classifier was rescaled to match behavior using previously published methods (Meyer & Rust, 2018).



Figure 1: Comparison of neural representations in spikes (top row) and HG (bottom row) in an example animal. A-B) Dynamics of memory signals, reflected as repetition suppression (RS), C-D) RS in individual units or channels, E-F) RS as a function of n-back, G-H) Response magnitude as a function of memorability, I-J) Dynamics of contrast modulation.

Results

Spikes and HG are well-aligned

Memory A memory signal in ITC is thought to be repetition suppression: the tendency for ITC's population response magnitude to be reduced the second time an image is presented compared to the first (Figure 1A). Like spikes, HG showed robust repetition suppression that emerged after 100 ms (Figure 1B) and was observed across most individual units (Figure 1C) and channels (Figure 1D). Animals with less spike repetition suppression also had less HG repetition suppression, further suggesting that HG captures the underlying population spiking activity. Repetition suppression in both spikes (Figure 1E) and HG (Figure 1F) tended to decrease as the number of intervening images between the novel and repeated presentation (n-back) increased.



Figure 2: HG predicts memory as well as spikes. A) Behavior plotted with neural predictions from spikes (red) and HG (blue) for one monkey (solid point in B). B) Error between neural predictions and behavior across all monkeys.

Memorability Some images are consistently better remembered than others, an intrinsic property known as memorability (Khosla et al., 2015). Spike population response magnitude in ITC has been shown to correlate with memorability (Jaegle

et al., 2019) (Figure 1G, r = 0.80). Strikingly, HG also correlated strongly with memorability (Figure 1H, r = 0.78). Again, animals with smaller memorability correlations in spikes also had smaller correlations in HG, and the dynamics of the HG response closely matched that in the spikes.

Contrast Similar to other studies of spike and HG contrast modulation (Ray & Maunsell, 2011) in earlier visual areas, we found that spike population magnitude (Figure 1I) and HG (Figure 1J) in ITC were similarly modulated by image contrast. Once again, animals with larger effects of contrast in spikes showed larger effects in HG.

Neural representations in spikes and HG both predict visual memory behavior

Memory performance tends to decrease as n-back increases (Figure 2A). To directly link neural representations to memory behavior, we trained a cross-validated linear decoder to predict memory performance. We replicated previous work showing that the decoder trained on spike data can predict memory (Meyer & Rust, 2018) and extended this to show that HG representations are also predictive of behavior (Figure 2A). Across monkeys, decoders trained on HG predicted behavior as well as those trained on spikes (Figure 2B).

Conclusions

The same inferences about the neural mechanisms of visual memory would have been made with HG or spikes. In fact, HG and spikes are so strongly aligned that HG directly predicts memory behavior as well as spikes (Figure 2). These findings suggest that variables that influence overall population firing (like memory, memorability, and contrast) may be good targets for observation in LFPs and supports the hope that insights from animal studies may translate to human recordings, where spike recordings are often absent or limited.

Acknowledgments

This work was supported by the National Eye Institute of the NIH (award R01EY020851 to N.C.R.) and the Simons Foundation (Simons Collaboration on the Global Brain award 543033 to N.C.R.).

References

- Chang, E. (2015). Towards Large-Scale, Human-Based, Mesoscopic Neurotechnologies. *Neuron*, *86*(1), 68–78.
 (Publisher: Elsevier) doi: 10.1016/j.neuron.2015.03.037
- Henin, S., Shankar, A., Hasulak, N., Friedman, D., Dugan, P., Melloni, L., ... Liu, A. (2019). Hippocampal gamma predicts associative memory performance as measured by acute and chronic intracranial EEG. *Scientific Reports*, 9(1), 593. doi: 10.1038/s41598-018-37561-z
- Jacobs, J., & Kahana, M. J. (2010). Direct brain recordings fuel advances in cognitive electrophysiology. *Trends in cognitive sciences*, 14(4), 162–171. (Place: England) doi: 10.1016/j.tics.2010.01.005
- Jaegle, A., Mehrpour, V., Mohsenzadeh, Y., Meyer, T., Oliva, A., & Rust, N. (2019). Population response magnitude variation in inferotemporal cortex predicts image memorability. *eLife*, 8, e47596. doi: 10.7554/eLife.47596
- Khosla, A., Raju, A. S., Torralba, A., & Oliva, A. (2015). Understanding and Predicting Image Memorability at a Large Scale. In 2015 IEEE International Conference on Computer Vision (ICCV) (pp. 2390–2398). Santiago, Chile: IEEE. doi: 10.1109/ICCV.2015.275
- Kreiman, G., Hung, C. P., Kraskov, A., Quiroga, R. Q., Poggio, T., & DiCarlo, J. J. (2006). Object Selectivity of Local Field Potentials and Spikes in the Macaque Inferior Temporal Cortex. *Neuron*, 49(3), 433–445. doi: 10.1016/j.neuron.2005.12.019
- Liu, J., & Newsome, W. T. (2006). Local Field Potential in Cortical Area MT: Stimulus Tuning and Behavioral Correlations. *The Journal of Neuroscience*, 26(30), 7779–7790. doi: 10.1523/JNEUROSCI.5052-05.2006
- Mehrpour, V., Meyer, T., Simoncelli, E. P., & Rust, N. C. (2021). Pinpointing the neural signatures of single-exposure visual recognition memory. *Proceedings of the National Academy of Sciences*, *118*(18), e2021660118. doi: 10.1073/pnas.2021660118
- Meyer, T., & Rust, N. C. (2018). Single-exposure visual memory judgments are reflected in inferotemporal cortex. *eLife*, 7, e32259. doi: 10.7554/eLife.32259
- Parvizi, J., & Kastner, S. (2018). Promises and limitations of human intracranial electroencephalography. Nature Neuroscience, 21(4), 474–483. Retrieved from https://doi.org/10.1038/s41593-018-0108-2 doi: 10.1038/s41593-018-0108-2
- Ray, S., & Maunsell, J. H. R. (2011). Different Origins of Gamma Rhythm and High-Gamma Activity in Macaque Visual Cortex. *PLoS Biology*, *9*(4), e1000610. doi: 10.1371/journal.pbio.1000610

- Sederberg, P. B., Schulze-Bonhage, A., Madsen, J. R., Bromfield, E. B., McCarthy, D. C., Brandt, A., ... Kahana, M. J. (2007). Hippocampal and neocortical gamma oscillations predict memory formation in humans. *Cerebral cortex (New York, N.Y. : 1991)*, *17*(5), 1190–1196. (Place: United States) doi: 10.1093/cercor/bhl030
- Urai, A. E., Doiron, B., Leifer, A. M., & Churchland, A. K. (2022). Large-scale neural recordings call for new insights to link brain and behavior. *Nature Neuroscience*, 25(1), 11– 19. doi: 10.1038/s41593-021-00980-9