## Behaviorally-locked structure in a sensory neural code

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Firing rates, covariances, and population activity distributions of sensory neurons are all frequently used to characterize neural codes. However, while such characteristics are often studied, their relation to the time-dependence of sensory stimuli and sampling behavior is often ignored. We show here an example where strong, behaviorally-locked structure in a neural code can be missed if the behavioral coupling is ignored.

We studied simultaneous recordings of sniffs and spikes<sup>1</sup> (in the absence of presented odors) from awake, headfixed mice (figure 1a). We found that the distributions of population activity patterns between and during<sup>2</sup> sniffs were nearly indistinguishable (figure 1b). However, when we further subdivided the during-sniff activity into "sniff phases",<sup>3</sup> the sniff phase-dependent distributions were easily distinguishable from one another (figure 1c), especially for non-adjacent phases, and from the between- and during-sniff distributions (figures 1d and 1e). Partially responsible for these differences were strong ( $\approx .05$  to .25 in absolute value) but transient covariances in the neural firing rates. Consistent with these results, we found that the sniff phases were characterized by as few as 25-50 common ( $p > 10^{-6}$ ) or 5-10 very common ( $p > 10^{-2}$ ) activity patterns,<sup>4</sup> many of which were not shared by the other phases ( $\approx 10\%$  to 50\% of the common patterns and > 50% of the very common patterns).

Together, these results reveal a highly structured, behaviorally-locked neural code that is not obvious when the neural activity is averaged across behavior. Our results suggest that sniff phase may be inferred from local neural activity in the olfactory bulb without requiring an efference copy of the sniff motor command.

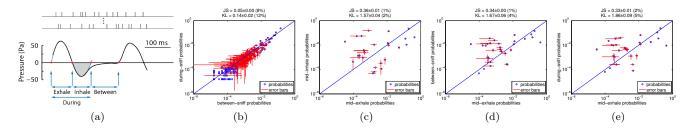


Figure 1: (a) Schematic of data collected. Spike trains above in grey. Sniff below in black. (b)-(e) Comparisons of various population activity distributions. Jensen-Shannon (JS) and Kullback–Leibler (KL) divergences plotted above each figure with error bars and percentage errors. Error bars were obtained by subsampling the data sets. Mid-exhale and mid-inhale activity were defined as the middle 20ms of each exhale or inhale. Similar results were obtained for other sniff phases (e.g. beginning/end of exhale/inhale).

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<sup>&</sup>lt;sup>1</sup>Sniffs were obtained from intranasal pressure sensors. Spikes were obtained from extracellular recordings of 9-11 mitral/tufted cells in the olfactory bulb. Quoted numbers and figures are from a 9-cell data set, though similar results were obtained for other data sets. <sup>2</sup>The during-sniff period was defined to include both the exhale and inhale (figure 1a).

 $<sup>^{3}</sup>$ The exhale and inhale were each divided into three roughly equal periods (six total) for each sniff.

 $<sup>^4\</sup>mathrm{Probabilities}$  were calculated using 10ms bins.