Supplementary Information for

Correlated input reveals coexisting coding schemes in a sensory cortex

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Content:
- Supplementary Figures 1-12
- Supplementary Table 1
Supplementary Figure 1. Characterization of the stimulus used to build LN models. (a) Black and grey dots: independently stimulated whiskers (and Stradlers in grey) during the experiment. Red arrows: Rostro-Caudal axis of deflection and position of the resting angle. \( \rho \): deflection angle. (b) Stimulus input command (red) and corresponding motion of one piezoelectric actuator (blue). (c) Power spectral density of the command and of the actual motion. 3 dB bandwidth: 82 Hz. (d) Stimulus angular position distributions during Gaussian noise. Stimulus amplitudes are in the same order of magnitude as the “stick and slip” motions that occur frequently in freely behaving animals. In particular, they compare well with the literature that describes the ‘stick and slips’ mechanical properties. (e) Stimulus angular speed distribution during Gaussian noise. This distribution is comparable to the magnitude reported in the “stick and slip” literature. In particular, under a rigid whisker assumption, it was found [Wolfe et al. 2008, PLOS Biol e215] that the average “stick and slip” deflection to be around 3° wide and to have a top speed of 540°/s (both values are comparable to our explored range). A second study [Jadhav et al. 2009, Nat Neurosci 12:792-800] observed “stick and slip” motions in the range 300-2000°/s (which includes our range of explored values). Finally, a third study [Ritt et al. 2008, Neuron 57:599-613] found a mean “stick and slip” amplitude of 0.98° which is within our explored range. However, the mean speed was 1612°/s in that study, a value that could not be reached by our stimulator.
Supplementary Figure 2. Effect of stimulus frequency bandwidth and ridge regression (regularization) on the estimation of neurons functional properties. The frequency content of the linear filters extracted from a reverse correlation analysis reflects the frequency tuning curve of the neurons, but it depends also on the frequency content of the whisker stimulation used to perform this analysis. To ensure that the Gaussian noise stimulus bandwidth used during the experiments was sufficient to sample adequately the functional response of barrel cortex neurons, we compared the functional responses obtained with three stimulus bandwidths: 0-60 Hz (red), 0-83 Hz (green) and 0-100 Hz (blue), 0-83 Hz being the bandwidth of the stimulus used in the rest of the study. (a) Simple neurons linear filter (top left) and non-linear functions (top right and bottom) for the three different frequency bandwidths. Overall, the linear filter peak frequency and the non-linear filter sharpness in the resulting LN models were both affected by changing the bandwidth, although the basis of our functional classification was unaffected: a simple neuron displayed the same phase selectivity across different bandwidth, as seen in its linear and non-linear filters. (b) Simple cell (top) and complex cell (bottom) LN model estimated with a 0-83 Hz frequency bandwidth before/after regularization of the stimulus ensemble based on a ridge regression [Smyth et al. 2003, J Neurosci 23:4746-4759, Theunissen et al. 2000, J Neurosci 20, 2315-2331] (ridge parameter $\lambda = 5.5 \times 10^5$). (c) Population analysis of linear filters peak frequency as measured with the three bandwidths (N = 85). Red and green curves: average tendencies. Arrowhead: average values. The frequency difference between the filters sampled with the 0-100 Hz vs 0-80 Hz bandwidth was smaller than between the 0-83 Hz and 0-60 Hz bandwidths (7 Hz difference versus 11 Hz difference). This suggests that an ideal bandwidth to sample barrel cortex neuron properties may be only slightly wider than the 0-83 Hz used across the study. (d) Same as in (c) but with a regularized STC analysis. As expected, regularized linear filters display higher peak frequencies (mean frequency for the 0-83 Hz bandwidth: 53 Hz, compared to 43 Hz for a non-regularized STC). In addition, non-linear filters are sharper, and regularization does not affect the units’ functional type. Most importantly, the population analysis of the frequency of the regularized linear filters shows an improved correspondence between the linear filter frequencies obtained with the 0-83 Hz bandwidth and with the 0-100 Hz bandwidth (compare (c) and (d)) even if filters with high peak frequencies were still underestimated, as previously reported [Smyth et al. 2003, J Neurosci 23:4746-4759].
Supplementary Figure 3. Playback stimulus frequency effect on evoked activity. (a) Single unit PSTHs produced by applying playback stimulations of the common linear filter 1 with carrier frequency 36 Hz (red), 48 Hz (green) and 60 Hz (blue). (b) Same as a for a different neuron with broader PSTHs response. (c) Normalized difference between the amplitude of functional responses to playback stimuli displaying a 36 Hz vs 60 Hz carrier frequencies (black dots) or 48 Hz vs 60 Hz carrier frequencies (empty circles) as a function of the PSTH full width at half weight (N = 54). Continuous and dashed line: corresponding linear fits.
Supplementary Figure 4. Filter properties across neuronal population with significant sensory responses. (a) All significant mono-whisker linear filters obtained using STC across all neurons and protocols, vertically sorted by their phase in the subspace spanned by the two common linear filters of Figure 1d (680 linear filters, common filters are shown in dashed lines for both directions) (b) Distribution of the phase difference between the first two significant filters across all neurons with at least two significant filters. (c) Comparison between the optimal LN model obtained by individual STC and the LN model in the common subspace. For 2 selected neurons, the linear filters estimated with STC (red and blue continuous line) are compared to their approximation in the common space (red and blue dashed line). As visible on the projection of all linear filters into the common space (left), these examples correspond to the situation where the linear filters are well approximated by the common filters (neuron 1, filled dots) or to the situation where the linear filters are not completely described by the common filters (neuron 2, empty dots). The corresponding 2D non-linear functions (right) are depicted for both cells and functional sub-space (original subspace versus common filters subspace).
Supplementary Figure 5. Relationship between phase tuning and classical directional tuning. (a) It could be possible that the phase tuning results from a simple readout of the classical 2D directional tuning. We tested this hypothesis by measuring (N=33 simple neurons with C2 as their principal whisker) both the phase tuning of neurons in the rostrocaudal axis (Right) and their directional tuning in the rostro-caudal/ventro-dorsal plan by applying Dirac pulses in 8 directions. (b) Directional and phase tuning of 9 neurons (8 simple cells and 1 complex cell) with sharp directional tuning in response to C2 whisker deflections and representative of the response diversity. For each neuron, the left plot is the directional tuning, with on the margins the PSTHs obtained for each directional stimulus and the left plot is the phase tuning (non-linear function in the phase space) of the neuron. Green lines: average directional/phase tuning. (c) Left: scatter plot of the average phase versus average directional tuning (n=33 simple neurons). The 8 simple cells presented in b are indicated with black squares. Notice that phase/direction pairs are scattered and not clustered on a monotonic curve (circular correlation coefficient: 0.46). Right: scatter plot of the average phase versus tuning index in the Rostro-Caudal axis (R-C)/(C-R) obtained on the mean firing rate during the ON response to the Dirac stimulus (circular corr. coefficient: -0.55). Neither directional tuning (21% of phase variance explained) nor rostrocaudal axis directional tuning (30% of explained variance) can account alone for the neurons phase tuning.
Supplementary Figure 6. Position/Speed selectivity within the phase space. A previous study in the whisker system [Petersen et al. 2008, Neuron 60: 890-903] has shown that many neurons in the VPM nucleus can generally be described either as position-selective or speed-selective selective cell (or a combination of those two features). To understand the link between the 2D phase space that we described here and this position/speed sensory space, we focused on neurons clearly biased towards one specific phase. We applied on such neurons both “Position-biased stimuli” that are going either to rostral or caudal angles (positions), but are symmetric in terms of deflection speed (c, right panel) and “Speed-biased stimuli” that spend as much time in rostral and caudal angles, but are biased in terms of speed either in the rostral or caudal directions (c, left panel). (a) LN model of a speed selective neuron. (b) 2D non-linear function of a neuron tuned close to the speed selective axis (blue axis). (c) Top: Speed (left) and position (right) biased stimuli are applied to the LN model of a speed-selective neuron (middle) and to the neuron in b (bottom). Note the similarity between the response of the neuron and the predictions of the speed-selective LN model. (d) LN model of a position selective neuron. (e) 2D non-linear function of a neuron tuned close to the position selective axis (green axis). (f) Same as c for model in d and neuron in e. Note the similarity between the response of the neuron and the predictions of the speed-selective LN model. These properties can be related to the fact that in the phase space that we describe, one dimension corresponds to a biphasic filter with a null sum (roughly the first dimension, more precisely the blue axis in a) that is a differentiator – a filter selective for speed. The second common filter is closer to an integrator (specifically the green axis in a), meaning a filter mainly biased toward whisker position instead of the speed of the stimulation.
Supplementary Figure 7. As a comparison point with previous forward-correlation studies of rat barrel cortex receptive fields [Simons et al. 1978, J. Neurophysiol 41: 798-820, Brecht et al. 2002, J. Physiol 543: 49-70, LeCam et al. 2011, J. Neurophysiol 106: 986-998, Manns et al. 2004, J. Physiol 556: 601-622], we applied on a subset of neurons a classical forward correlation sparse stimulation using 'rostral' and 'caudal' Dirac-like deflections with a 30 ms repetition rate (a-c & e-f) in addition to the Gaussian-noise stimuli. (a) Sparse noise stimulations. In this protocol, each whisker is stimulated randomly with Dirac-like deflections, either in rostral or caudal directions, with no overlap with other whisker deflections (30 ms repetition rate). Surprise was computed as follows: a Poisson process with average firing rate defined by the spontaneous neuronal firing rate was used to evaluate the probability of occurrence of the neuron response. This response was defined as the mean firing rate over a 20 ms time window centered on the peak after stimulation onset. The measurement (-log10(Poisson p-value(firing rate))) was then computed. (b) Map of the maximum surprise response of a Global neuron across whisker pad, for rostral (orange) and caudal (purple) deflections. (c) Count of significant whiskers in the surprise maps across all Global neurons that were submitted to the sparse stimulus. (d) Population baseline firing rate across all Global neurons (N = 75). (e-g) Same as b-d for Local neurons, significantly lower than Global neurons firing rate (N = 147, Mann-Whitney p = 3.0x10^{-7}). Overall, Global neurons displayed extended receptive fields with up to 6 significant whiskers (b-c), but with a limited response amplitude. In contrast, Local neurons (e-f) responded strongly to a significantly lower number of whiskers (Mann Whitney p = 2.7x10^{-3} with N = 16 Local neurons and N = 12 Global neurons). (h) Population baseline firing rate across all Simple neurons (N = 90). (i) Same as h for Complex neurons, significantly higher than Simple neurons firing rate (N = 281, Mann-Whitney p = 1.0x10^{-9}).
Supplementary Figure 8. Histological identification of electrode recording sites. (a) Background image: flattened and cytochrome oxidase stained barrel cortex at layer IV. Barrels are shown in black and the septum in light grey. Red: Dil fluorescent marks left by the electrode shanks. (b) Three-dimensional reconstruction of barrels (gray polygons circled in blue), electrode track (black line) and recording points (red crosses) through histological slices. (c) For neurons recorded during experiments that included successful histological reconstruction (N = 159), the proportion of Local/Global neurons is shown across barrel cortex deep layers. Within each layer and compartment, the proportion of Simple/Complex neurons is gray shade coded. (d) Population distribution across cortical depth as assessed by the micromanipulator is shown for Local Simple (N = 42), Local Complex (N = 105), Global Simple (N = 6) and Global Complex (N = 69) functional cell types.
Supplementary Figure 9. Response comparison between center-only (principal whisker) and whisker-pad-wide uncorrelated stimulations. (a) Response of a neuron to the first common filter when played on the neuron center (principal) whisker in both directions (orange and purple), during four different protocols. From left to right: all whiskers are correlated; the stimulus is applied only on the principal whisker; all whiskers are uncorrelated; antagonist stimuli are applied on center and surround whiskers. (b) Population comparison of the amplitude of the response between uncorrelated stimulation and single whisker stimulation on the principal whisker, for both directions of stimulation (N = 27).
Supplementary Figure 10. Confirmation of the functional properties of Local neurons in response to uncorrelated versus correlated stimulations. (a) Non-linear function (projected onto common filter 1) of a Local neuron obtained with uncorrelated (gray) and correlated (black) stimulations. Color-coded (orange and purple) waveforms on bottom sides of the graph indicate direction in the filter 1 subspace. (b) Top: spatially uncorrelated playback of the first common filter on both directions (orange and purple) presented with Poisson intervals between occurrences (see Methods). Bottom: corresponding PSTHs measured for both directions. (c) Same as b for spatially correlated stimulations. (d) Comparison of the firing rates between measured PSTH and PSTH predicted using the LN model, for both directions (purple and orange waveforms), and correlation levels (top: uncorrelated, bottom: correlated, 20 ms time bin). (e) PSTH measured during uncorrelated natural stimulation (red) and the corresponding LN-model prediction (green) in a Local neuron (20 ms time bin). (f) Distribution of the Pearson coefficients between PSTHs measured for multiple replays of a continuous uncorrelated natural stimulation and the corresponding LN model predictions (N = 24, mean Pearson coefficient: 0.5). PSTHs are computed with a 20 ms time bin.
Supplementary Figure 11. Impact of cortical state on neurons functional properties. (a) Functional responses under two stages of anesthesia. The level of anesthesia is known to affect the strength and temporal dynamics of the functional responses observed in the rat barrel cortex [Simons et al. 1992, Exp. Brain Res. 91: 259-272]. To characterize the impact of anesthesia on the functional response obtained during the experiments, we characterized the functional response of neurons (N = 40) under two stages of anesthesia [Friedberg et al. 1999, J Neurophy 81: 2243-2252]. First, the stage at which the recordings were obtained through this work; Stage III, plane ½, corresponding to high frequency (> 5 Hz) ECoG. (2) quite (1-1.5 Hz) and stable breathing and the absence of whisker and limb spontaneous movement. Second a deeper stage of anesthesia that was stable over long recording periods: Stage III, plane 4, characterized by the occurrence of spindles (short bursts) and a quite (0.5-1 Hz) and stable breathing. Top: isoflurane concentration. Middle: examples of single units (red) and multi-units (gray) spiking activity and below the electro-corticogram (ECoG) and the corresponding spectrogram used to identify the cortical state during these two conditions (bottom). (b) Non-linear functions of a Global Complex neuron (left) and a Local Simple neuron (right) recorded during cortical state III-1/2 or III-4 and during correlated or uncorrelated stimulations. (c) Population comparison of the linear filters significance (Z score) of Global neurons (N = 22, gray) and Local neurons (N = 18, black) between uncorrelated (left panel) or correlated (right panel) stimulations and during cortical state III-1/2 or III-4. Dashed black lines: a Z score of 8 standard deviations defines the significance threshold. Functional responses were systematically lost with deeper anesthesia.
Supplementary Figure 12. Adaptation to changes in input statistics. Adaptation to changes in stimulus local properties such as the amplitude of whisker deflection have been already reported in the whisker system [Maravall et al. 2007, PLOS Biol 5: e19]. In the present study we observed adaptation to changes of the spatial second-order properties. This was particularly visible when we applied sequentially anticorrelated and correlated stimulations without any temporal gap (a) Center/surround phase tuning map of a Local Simple neuron. Arrows depict the studied transition from center/surround correlated Gaussian noise (green line) to anti-correlated Gaussian noise (blue line) stimulations. (b) PSTH for the transition from correlated to anti-correlated Gaussian noise stimulation. (c) PSTH for the transition from correlated to anti-correlated Gaussian noise stimulation showing adaptation of the firing rate following the fast firing rate change when transitioning from one spatial statistic to the next.
Supplementary Table 1. Summary of neurons recorded during the study. (a) Neurons count across Local/Global and Simple/Complex categories. Darkest gray: for each category, neuron obtained during recordings including both uncorrelated and correlated stimulations (as required to detect both Local and Global neurons in the same experiment). (b) Neuron count for the 8 additional protocols/experiments carried on different subsets of the studied neurons. (c) Neuron count for 5 additional experiments studying the link between directional selectivity and phase selectivity.