## Global and Local Neuronal Coding of Tactile Information in the Barrel Cortex

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### Abstract

During tactile sensation in rodents, whisker movements across surfaces generate complex whisker motions that include discrete, transient stick-slip events, which transmit information about surface properties. These surface characteristics are transformed into cortical neuronal responses. In this study, we examined the different coding strategies underlying these transformations in the rat somatosensory whisker system. We found that changes in surface coarseness resulted in two main modifications in the transformation of stick-slip events into neuronal discharges: the number of stick-slip events that resulted in spikes and the magnitude of these events. Global changes in the number of stick-slip events primarily affected neuronal discharge rates and the degree of neuronal synchronization. In contrast, local changes in the magnitude of stick-slip events affected the transformation of these events' kinematic and kinetic characteristics into neuronal discharges. Most cortical neurons exhibited surface coarseness preference through global and local coding. However, this preference varied across coding strategies in the same neurons given that each coding strategy reflected different aspects of changes in whisker-surface interactions. The degree of spatial similarity in surface coarseness preference in adjacently recorded neurons differed among these various coding strategies. Adjacently recorded neurons exhibited the same surface coarseness preference in their firing rates but not through other coding strategies. Through these results, we were able to show that local coding contributes to texture discrimination, complementing and surpassing global coding in this context. These findings suggest that the representation of surface coarseness in the cortex may rely on concurrent coding strategies that integrate tactile information across different spatiotemporal scales.

**Significance**

When we interact with the world, our sensorimotor system processes extremely large volumes of information. Using these sensory inputs, we can construct an internal representation of the environment, enabling us to accurately interact with a complex, changing environment. The present results suggest that this process may be accomplished through the ability of neurons to convey multiple tactile parameters through coexisting coding strategies. Notably, different modes of sensory transmission revealed preferential selectivity for various stimulus features. These multi-layered coding schemes enable spike trains to convey information regarding a stimulus through multiple complementary channels, each corresponding to a different aspect of the sensory world and its variations.

**Introduction**

Rodents use their whiskers to detect and distinguish various tactile features in their environment [[1](#_ENREF_1), [2](#_ENREF_2)], including object positions [[3-5](#_ENREF_3)], shapes [[2](#_ENREF_2), [6](#_ENREF_6)], aperture and gap widths [[7](#_ENREF_7)], and textures [[8-14](#_ENREF_8)]. The active and receptive interactions between the whiskers, given their specific properties [[15-17](#_ENREF_15)], and the environment result in frictional movement and induce whisker bending, vibrations, and brief, discrete micromotions referred to as stick-slip events (SSEs) [[13](#_ENREF_13), [18-23](#_ENREF_18)]. The role of the somatosensory system is to decode this information in a manner that enables the accurate determination of the location, shape, and contours of the sensed object.

Several models for the neuronal encoding of surface coarseness in the whisker somatosensory system have been proposed. In one model, the representation of surface coarseness results from the temporal integration of whisker vibration signals within relatively extended ranges. Specifically, this representation is related to the mean speed of surface-induced whisker vibrations [[24-26](#_ENREF_24)] and is encoded in the mean firing rate of vibrissal somatosensory cortex (vS1) neurons [[21](#_ENREF_21), [24](#_ENREF_24), [27](#_ENREF_27), [28](#_ENREF_28)]. However, given that SSEs represent significant determinants of overall mean whisker speed, they may still serve as the primary textural cue as they generate most vS1 spikes [[13](#_ENREF_13), [21](#_ENREF_21), [25](#_ENREF_25), [29](#_ENREF_29)]. Another plausible coding strategy relies on precise spike timing through the spatiotemporal coordination and synchronization of neuronal assemblies. This synchronization enables neuronal ensembles to better encode specific stimulus features and may serve as an efficient and flexible coding mechanism for sensory and cognitive processing [[30-37](#_ENREF_30)]. Over the last several years, it has been shown that neuronal synchrony is prevalent in the barrel cortex and thalamus of anesthetized and awake rodents [[38-40](#_ENREF_38)]. This synchrony is present in both thalamic spike timing and membrane potentials in cortical neurons, which were shown to be highly correlated during active touch, thus pointing to a specific synchronization of functional subnetworks [[41-43](#_ENREF_41)]. Finally, recent findings indicated that SSEs may function as a coding strategy [[21](#_ENREF_21), [25](#_ENREF_25), [44](#_ENREF_44)]. In recent years, the kinematic profiles of SSEs have been reported to carry texture-related information [[21](#_ENREF_21), [44](#_ENREF_44)] and they are readily encoded by neurons of the ascending tactile pathway [[10](#_ENREF_10), [25](#_ENREF_25), [45-51](#_ENREF_45)]. These events evoke low-probability responses in vS1 neurons [[41](#_ENREF_41), [47](#_ENREF_47), [52-54](#_ENREF_52)], and these are clearly related to SSE magnitude [[46](#_ENREF_46), [55](#_ENREF_55), [56](#_ENREF_56)]. Thus, coding through SSEs differs distinctly from the former two strategies in its ‘local’ spatiotemporal character [[57](#_ENREF_57)].

In the present study, we compared the different cortical coding strategies for surface coarseness. To achieve this, we measured whisker vibrations in response to different textures and vS1 neural activity in anesthetized rats. We found that in addition to neuronal discharge rates, temporal coding is an essential feature of sensory-evoked activity in the barrel cortex. This coding is expressed in the temporal coincidence of a subset of the spikes in the neuronal population. These coincidences form a dynamically and functionally relevant subnetwork [[58-64](#_ENREF_58)]. Moreover, we found that vS1 neurons encoded SSE amplitude with sparse, low-probability, precisely timed spikes during continuous contact with surfaces. The transformation of SSEs into response probabilities and temporal aspects of neuronal responses may serve as a robust coding strategy for surface coarseness. These results suggest that multiple coding strategies can account for the multiple facets of surfaces and objects.

Materials and Methods

***Animals and Surgery***

Sprague Dawley rats (250–320 gm) were anesthetized with ketamine (100 mg/kg, i.p.; Ketaset; Fort Dodge Animal Health, Fort Dodge, IA) and acepromazine maleate (1 mg/kg, i.p; PromAce; Fort Dodge Animal Health). After tracheotomy, a short (1.5 cm) metal cannula [outer diameter (o.d.), 2 mm; inner diameter (i.d.), 1.5 mm] was inserted into the trachea. The rats were then placed in a standard stereotaxic device. Body temperature was kept at 37.0 ± 0.1°C using a heating blanket and a rectal thermometer (TC-1000; CWE, Ardmore, PA). Anesthesia was maintained using a mixture of halothane (0.5–1.5%) and air employing artificial respiration at a rate of 100–115 breaths/min while monitoring end-tidal CO2 levels and heart rate. Depth of anesthesia was monitored based on heart rate (250–450 bpm), eyelid reflex, pinch withdrawal, and vibrissal movements. Halothane concentrations were set slightly above the level at which the first clear signs of vibrissal movements were observed while the eyelid reflex was still maintained. In some animals, we also used EEG recordings obtained using two wires inserted under the skull at a distance of 10 mm anterocaudally. Based on these measurements, we determined the anesthesia level in our recordings to be between stages III-2 and III-3[[65](#_ENREF_65)]. After placing the subjects in a stereotactic apparatus (TSE, Bad Homburg, Germany), an opening (1-2 mm in diameter) was made above the barrel cortex (centered at 2.5 mm posterior and 5.2 mm lateral to the bregma), and the dura mater was carefully removed.

In some of the animals, we determined the correspondence between microdrive depth and laminar identity. We induced electrolytic lesions using the recording electrodes by applying a direct current (10-30 μA) for 4 s at a depth corresponding to each recorded area. In some of the rats, brain tissues were also processed for CO histochemistry. The animals were perfused transcardially with 2.5% glutaraldehyde and 0.5% paraformaldehyde, followed by 5% sucrose, all in 0.1M PBS (Phosphate Buffered Saline). Brains from these rats were then transferred to a 30% sucrose post-fixative solution and incubated overnight at 4°C. The following day, microtome cryosections (120 μm) were prepared and incubated in PBS containing 0.0015% cytochrome C (Sigma) and 0.05% diaminobenzidine 20 - 50 min at 37°C. The reaction was terminated by washing with PBS. CO-stained sections were mounted on gelatin-coated slides, air-dried, and coverslipped. Layers 2/3, 4, 5, and 6 were identified by recording depths of 150-550, 550-850, 900-1400, and 1400 μm and deeper, respectively.

All experiments were conducted in accordance with appropriate international standards and were approved by the Ben-Gurion University (BGU) Committee for the Ethical Care and Use of Animals in Research (project license: IL-71-11-2016). The BGU animal care and use program is supervised and fully assured by the Israeli Council for Animal Experimentation of the Ministry of Health. It is operated according to Israel’s Animal Welfare Act of 1994 and follows the Guide for Care and Use of Laboratory Animals (NRC 2011). In addition, BGU is approved by the Office of Laboratory Animal Welfare, USA (OWLA) (#A5060-01). Sprague Dawley rats (250-300 g) were used for all experiments described herein.

***Recording technique***

A multi-contact silicone electrode (NeuroNexus, Ann Arbor, Michigan) was inserted into the barrel cortex. The electrode was lowered using a precision stereotactic micromanipulator (TSE-systems, Germany). During recording, signals were amplified (1000x), digitized (25 kHz), filtered (0.1–10,000 kHz), and stored for offline spike sorting and analysis using the ME-16 amplifier and MC-Rack software (MEA, Germany). Data were then separated into local field potentials (LFP; 1-150 Hz) and isolated single-unit activity (0.5-10 kHz). All neurons could be driven by the manual stimulation of one of the whiskers. Spike extraction and sorting were implemented using the MClust (by A.D. Redish; http://redishlab.neuroscience.umn.edu/MClust/MClust.html) MATLAB (Mathworks, Natick, MA)-based spike-sorting software. The extracted and sorted spikes were stored at a 100 µs resolution, and peri-stimulus time histograms (PSTHs) were computed.

***Whisker stimulation***

To replay whisker movements across different surfaces during receptive sensing in awake behaving rats, we covered the face of a rotating cylinder with several grades of sandpaper with different degrees of coarseness and rotated the cylinder against the whiskers (Fig. 1A). The cylinder face was placed so that the whiskers of the subject rats rested upon it (Fig. 1A), and it was positioned to mimic rostral-caudal whisker movement during head movement. The head velocities associated with rat exploration were taken from Lottem and Azouz [[13](#_ENREF_13), [66](#_ENREF_66)][66](#_ENREF_66" \o "Gugig, 2020 #2061)[66666666](#_ENREF_66). Cylinder velocity was controlled using a DC motor driven at approximately 147 Deg/sec to replicate median *head velocity*. The 30 mm diameter wheel was driven by a DC motor (Farnell, Leeds, UK). Surfaces of five different coarseness grades were employed in this study (from coarse- to fine-grained; grain sizes in parentheses in microns): P120 (125), P220 (68), P400 (35), P600 (25), and P800 (21). These grades were selected based on previous studies [[11](#_ENREF_11), [25](#_ENREF_25), [67](#_ENREF_67)]. A Mikrotron CoaXPress 4CXP camera measured whisker displacements transmitted to the receptors in the follicle at 1600 fps at 4 Megapixel resolution. The camera was installed above the arena and thus provided an overhead view while texture-covered cylinders were at velocities corresponding to head movements (see above). All the movies were analyzed using the Janelia whisker tracker software [[68](#_ENREF_68)]. To calculate whisker curvature, which enables the calculation of forces acting on the whisker follicle [[15](#_ENREF_15), [69](#_ENREF_69), [70](#_ENREF_70)][70](#_ENREF_70" \o "Quist, 2012 #1107)[70707070](#_ENREF_70), we used the method previously reported by Towal et al. [[69](#_ENREF_69)] implemented in the Janelia whisker tracker software [[68](#_ENREF_68)]. For this analysis, curvature was measured at 10 points along the whisker and the maximum local curvature per image was extracted.

***Data analysis***

To examine the influence of surface coarseness on whisker motion and resulting cortical neuronal responses, we established a trial structure. The cylinder rotated for 500 ms for each texture and remained still for 1500 ms. This procedure was repeated 75-150 times. We then aligned the whisker responses and the corresponding neuronal responses to the beginning of cylinder movement to generate PSTHs (Fig, 1E, F).

The significance of the differences between measured parameters was evaluated using a one-way analysis of variance (ANOVA). When significant differences were indicated in the F ratio test (*P*<0.05), Tukey’s multiple comparisons method was used to determine those pairs of measured parameters that differed significantly from each other within a group of parameters (*P*<0.05 or *P*<0.01). The results are presented as the mean ± standard deviation (SD). Error bars in all the figures indicate the SD unless otherwise noted. To avoid cluttering some of these graphs, single-sided error bars were used.

***Receiver operating characteristics analysis***

We used signal detection theory (receiver operating characteristics [ROC] ROC analysis [[71](#_ENREF_71)]), to compute the probability that an ideal observer could accurately determine the differences among the different textures based on neuronal activity. For each measured texture pair, an ROC curve was constructed in the form of a two-dimensional plot of hit probability (y-axis) and the probability of a false-alarm (x-axis). To transform raw data into a measure of discriminability, we analyzed the distributions of neuronal firing rates across trials. Green and Swets (1966) demonstrated that the area under the ROC curve (AUC) corresponds to the performance expected of an ideal observer in a two-alternative, forced-choice paradigm, such as the one used in the present analysis. The ROC curve was calculated for the firing rate of a single neuron as a function of texture. We then averaged all AUC values of all neurons and all texture pairs in the different rows or arcs.

The firing rate in trial *k* is the spike count in an interval of duration *T* divided by *T*

The length *T* for the texture signal was set to *T*=500 ms.

To measure the significance level of P(correct) in the analyzed ensemble of cortical neurons, we took all possible texture comparisons for all neurons. We then shuffled these trials across the different stimuli. This procedure was then repeated 500 times. The significance level was set at 90% of this population, which was 0.53 (Fig. 7F, dashed lines).

***Texture selectivity***

A neuron exposed to several textures shows a higher firing rate for a particular texture, and this neuronal property is referred to as texture selectivity [[72](#_ENREF_72)]. An additional criterion for texture preference implemented in the current study was determining whether a specific texture had a significantly higher firing rate (or any other parameter) than all other textures. To calculate the texture selectivity of cortical neurons, we used the Selectivity Index (SI).

*SI=Max(Pi)-〈P(j)〉/Max(Pi)*

*where P is the firing rates; i = preferred Texture; j = All Texture excluding the preferred texture; Max(Pi) = maximal firing rate; 〈P(j)〉 = the average firing rates across all textures.*

To quantify the statistical significance of texture selectivity, we first calculated the SI for several textures using the SI formula outlined above. Then, we created surrogate data for each neuron by shuffling the firing rate of *n*×75 trials (each texture had 75 trials; *n* = number of textures) between the different textures and then calculating the average firing rate for each texture across 75 trials. This process was repeated 500 times, and each time we calculated the SI as above. This resulted in a total of 500 SI data points. We calculated the ‘mean + 3SD’ from this 500 SI data distribution. If the original SI was more significant than the surrogate SI (mean+3SD), this confirmed that the effect was not due to chance.

Some neurons exhibited a gradual increase or decrease in firing rates and other parameters as a function of surface coarseness (Fig. 7C, lower panels). To categorize neurons based on these patterns, we examined whether at least 3 out of 4 neuronal responses to textures exhibited ascending (up) or descending (down) firing rates, SR values, and local features characteristics.

***Cluster significance***

To examine the degree of spatial clustering of texture selectivity of neurons recorded from the same site (<150 µm). We devised a measure of similarity between adjacent neurons, termed the cluster value, which was calculated as the number of neurons selective to the same texture divided by the total number of neurons in a particular cluster.

To assess the significance level, we calculated all possible variations for the different numbers of neurons in a cluster (3 - 5 neurons) for 4 and 5 textures used in the current study. We calculated the expected probability for all possible variations in the different conditions.

We found that for 3 neurons, the respective significance levels for 4 and 5 textures were 0.49 and 0.56. Figure 8E shows the significance level for 3 neurons and 4 textures.

***Quantification of temporal synchronization***

To compute the cross-correlation of a spike train, we used the method described previously by Maldonado et. al.[[73](#_ENREF_73)]. We represented the spike train of each neuron as a binary time series with 1 ms resolution such that:

We then computed the cross-correlogram histogram (CCH) that represents the way in which two neurons tend to fire in conjunction with one another:

CCH()= (t)

where M represents the number of trials, N is the number of bins in the trial, and are the spike trains of cells 1 and 2 on trial *i*, and is time lag.

To quantify the temporal synchronization of the correlated firing rate which occurred within ±10 ms of the zero time lag, we used the significance ratio (SR). SR was computed as the ratio of two integral values: a peak value (P), representing the magnitude of the spike correlation, which is computed by taking the sum of the bins in the central 20 ms of the cross-correlogram that exceeds the 95% confidence limit, and a variance value (V) representing the expected occurrence of coincident spikes, which is computed from the sum of the central 20 ms in each histogram lying between the 99% confidence limit and the mean value of the correlogram. We computed the SR as follows:

SR=P/V

where

and

and where

where *X* is the mean value of all bins in the cross-correlogram, and is the standard deviation of all the bins in the corresponding control correlogram.

Each CCH was computed from the cross-correlation between each trial of two neurons and the corresponding cumulative correlogram was calculated. The SR value was computed for each CCH. For each experimental trial, we computed an equivalent pseudorandom trial (i.e. a random trial taken from 75 trials) and a shuffled trial obtained by randomly shuffling 75 trials.

### To further examine the influence of the temporal pattern of spikes and the significance of the temporal locking of spikes to the stimulus, we also computed an equivalent pseudorandom trial in which we shuffled the inter-spike intervals within each trial. We created surrogate data that included an equal number of spikes and the same ISI distribution in each trial. This procedure shuffled spike timing and eliminated temporal locking to the SSE while keeping the number of spikes and the ISI distribution constant. These two simulations were repeated 500 times for each CCH on each trial. This yielded 500 control SR values (pseudorandom and inter-trial shuffled) for each experimental CCH. We assigned a confidence limit for statistical significance by choosing the SR values in the control distribution that were greater than 99% of the values. An SR ratio greater than one was considered significant.

### *Synchrony-based selection*

To differentiate between synchronized and asynchronous spikes, we initially selected neurons that exhibited significant synchronized activity in their spike trains (see above). We calculated the time window for significant correlation (central peak in the CCH) for these neurons. In these neurons, we searched for spikes in the two neurons that showed an interneuronal inter-spike interval (ISI) smaller than the chosen time window. These spikes were considered synchronized spikes, whereas spikes in the two neurons that showed interneuronal ISI larger than the chosen time window were considered asynchronous spikes.

### *Spike-triggered average calculations*

The Spike-triggered average (STA) kernel was calculated by averaging the signal (whisker position, velocity acceleration, curvature) over a particular time window (kernel width = 20 ms) preceding each spike [[74](#_ENREF_74)]. Using different spike types as the trigger and drawing the spike-triggered ensemble from different signal components, we calculated STA variants, denoted STAsync and STAasync. For the STA of LFPs, we averaged the LFP signal over 20 and 7 ms preceding and following each spike, respectively.

***Detection and quantification of SSEs underlying spikes***

Active and receptive interactions between the whiskers and the environment lead to frictional movement and induce whisker bending, vibrations, and brief, discrete micromotions called SSEs. To examine the relationship between SSE characteristics and the different response properties, we detected the underlying SSE for each spike by quantifying the timing of each SSE based on the defined peak value that crossed the threshold, within 20 ms preceding each spike. The threshold used in the current study was the mean±3 SD (see Fig. 5A, inset). The amplitude of SSEs preceding each spike was calculated by measuring the peak-to-peak amplitude within ±10 ms of the largest peak. To further verify this method, we calculated the SSE-spike latency. We found that latencies were minimal at L4 (6.8± 0.8 ms (mean ± SD, *n* = 72 neurons). Latencies were longer at L2/3 (10.3 ± 0.9 ms, *n* = 82). L5 and L6 exhibited even longer latencies (9.5 ± 1.6 ms, *n* = 69; 13.6 ± 0.9 ms, *n* = 47, respectively) [[56](#_ENREF_56), [75](#_ENREF_75)][75](#_ENREF_75" \o "Narayanan, 2017 #2064)[75757575](#_ENREF_75).

***SSE-dependent firing rates***

After detecting SSEs that resulted in spikes, we calculated the number of spikes following each of these SSE. We examined the influence of SSE amplitude on the number of spikes within the next 30 ms window for asynchronous spikes (Fig. 4E).

***SSE-dependent firing probability***

To examine the influence of SSE amplitude on discharge probability, we set a dynamic threshold from which we detected whisker vibration events. At a specified threshold for each of these events, we inspected the number of spikes within the next 30 ms window. We calculated the probability of spike discharge for each threshold value by calculating the ratio of the number of spikes and the number of events (Fig. 4D).

***Stimulus-dependent LFP commencement***

For each sensory-evoked spike, we identified its underlying LFP. To detect each LFP commencement, we calculated the 2nd derivative of the LFP. The 2nd derivative gave us the inflection point (red arrows in Fig. 5B, inset). From these points, we calculated the time interval between the sensory-evoked commencement of the LFP and the spikes.

### Results

To examine the transformation of whisker interactions with surfaces into cortical neuronal discharges, we replayed receptive whisker sensing of different surfaces by covering the face of a rotating cylinder with several grades of sandpaper with varying degrees of coarseness [[29](#_ENREF_29)]. The cylinder face was placed orthogonally to the vibrissae such that they rested upon it (Fig. 1A). The experimental goal was to collect records of the movement of whiskers across surfaces and use them as a stimulus set to probe the neuronal representation of surface coarseness [[13](#_ENREF_13)]. In the current study, we examined several measures of cortical neuronal responses to different textures. We recorded local field potentials (LFPs) and spikes with multi-site silicon probe electrodes from vS1 neurons. Single-neuron spike trains were isolated by spike sorting (see Methods section). After separating the spike trains arising from different neurons, the sample consisted of 270 paired recordings in all layers (supragranular: n = 82; Layer 4: n = 72; infragranular: n = 116). We recorded responses to five textures and measured neuronal discharge rates, spike count correlations, neuronal synchronization, and neuronal responses to SSE as a function of surface coarseness.

An example of whisker motion for two textures is shown in Figure 1B. We quantitatively evaluated the changes in whisker angle and curvature caused by texture coarseness. We first calculated the whiskers' position and the curvature SD of each measured whisker vibration in response to all studied textures to quantify these changes (the SD of these signals was calculated throughout stimulus duration: 500 ms). We quantified the range of whisker vibration in response to the different textures. As shown in Figure 1C (left panel), a relationship was observed between texture coarseness and whisker response characteristics. Coarser and finer surfaces are respectively expressed by higher and lower response SD values [[66](#_ENREF_66)]. These results were consistent across recordings for all whiskers (Fig. 1C right panel; *n* = 20) and suggest that the amplitude of SSE changes globally due to surface coarseness [[21](#_ENREF_21), [66](#_ENREF_66)].

Paired cortical neuronal responses to the different textures are shown in Figure 1D, while the PSTHs in Figure 1E shows the neuronal responses to four different textures. These examples corroborate our previous findings that different cortical neurons respond differently to various textures [[72](#_ENREF_72)]. We quantified the neuronal responses in Figure 1E, demonstrating that the first neuron reduces its firing rate monotonically as a function of surface coarseness. In contrast, the second neuron shows selectivity to P400 (see below).

We tested whether SSEs could provide a code for surface coarseness. Such an SSE code is plausible given that sharp, high-acceleration events effectively drive spikes in the somatosensory cortex [[21](#_ENREF_21), [25](#_ENREF_25), [56](#_ENREF_56), [76](#_ENREF_76)]. The pattern of SSEs will thus likely be encoded in the cortex. We used acceleration to identify these events [[21](#_ENREF_21)]. We compared acceleration events on four sandpaper textures. This measurement was performed for the C2, C3, D2, D3 whiskers (n = 20). For this analysis, an acceleration event was defined as any acceleration peak that crossed a defined threshold. We normalized each signal to the Z-score, so our threshold was reported in units of SD. We defined low-acceleration events as events occurring at a threshold of 0.05-0.25 SD. In contrast, high-acceleration events occurred at a threshold above 0.5 SD. We calculated the ratio between the two and found that high-acceleration events may systematically occur more frequently on rougher surfaces (Fig. 1H). These results highlight a gradual relationship between texture coarseness and the ratio between low/high acceleration events.

We characterized the SSE underlying spikes to further examine the transformation of whisker motion into cortical neuronal discharges. Figure 1F shows the distribution of SSE amplitudes underlying all the spikes of the neurons in Figure 1D-E. The number of events corresponds entirely with the firing rates. In contrast, the distribution of SSE amplitudes of the first neuron exhibits a bimodal distribution (upper panels), whereas the second neuron displays a unimodal distribution (lower panels). Comparing SSE amplitudes in response to the different textures (Fig. 1G) to firing rates reveals differential changes in the two separate neuronal response characteristics. We will analyze these phenomena later and discuss their relevance to additional coding strategies (Figs. 2-5).

***Texture-dependent spike timing correlations***

To examine whether cortical neuronal correlations carry information about surface coarseness, we recorded 270 neuronal pairs. Paired cortical neuronal responses to the different textures are shown in Figure 2A. The established PSTHs demonstrate the neuronal responses to four different textures. To examine the temporal synchronization between these pairs, we calculated the cross-correlation histogram between their spike trains (CCH; Fig. 2B).

To determine the statistical significance of the temporal synchronization, we computed an equivalent pseudorandom spike train for each pair of neurons. Figure 2B shows the CCHs for simultaneously recorded neurons (upper and lower panels in Fig. 2A). These CCHs exhibited a clear peak centered on zero time lag, as did all synchronized pairs, indicating that the spike timing correlation was attributable to common synaptic input rather than a direct connection between neurons [[77](#_ENREF_77)]. For this pair, the CCH was dependent on surface coarseness: the peak of the CCH was different for the different textures. To quantify the degree of synchrony, we calculated the synchronization ratio (SR) by dividing the magnitude of the original CCH by the confidence limit (selection criterion derived from the pseudorandom spike trains; see Methods section). An SR value larger than one was considered statistically significant. The properties of barrel cortex neuronal synchrony and a detailed analysis of this kind of activity have been described elsewhere [[38-43](#_ENREF_38)]. The incidence of significant response synchronizations for all neurons taken from the same tetrode for all conditions is summarized in Figure 2D. We found that out of the 270 pairs, 146 pairs (54%) showed significant temporal correlations in their spike trains (SR > 1). Figure 2C depicts the relationship between surface coarseness and discharge rates of the two recorded neurons and the SR values. These examples show that cortical neurons show changes in neuronal synchrony as a function of surface coarseness. These results indicate that neuronal synchronization with millisecond precision is a prevalent and robust feature of stimulus-evoked activity.

Since the SR values, in essence, reflect the proportion of synchronous spikes to what would be expected by chance, the responses of each neuron will be composed of synchronous and asynchronous spikes. All coincident spikes occurring within the significant temporal window determined by the CCH width for each neuronal pair (Fig. 2B) were designated as synchronous, while all other spikes were deemed asynchronous. Inspection of the SSE amplitudes underlying all the spikes revealed a bimodal distribution (Fig. 2E) in which the two types of spikes were expressed in significantly non-overlapping peaks. Thus, SSE amplitudes underlying synchronized spikes were larger than the SSE amplitudes underlying asynchronous spikes in all neurons [[56](#_ENREF_56)]. Further examination of SSE amplitudes in response to different textures revealed a rightward shift in the distribution of SSE amplitudes in response to coarser textures, consistent with Figures 1F-G. Coarser surfaces resulted in a rightward shift of SSE amplitudes that led to spikes.

This shift was consistent across all neurons. Inspection of the distribution of SSEs resulting in spikes for the different surfaces revealed that in addition to the shift in overall SSE magnitude as a function of surface coarseness, the number of asynchronous and synchronized SSEs resulting in spikes was altered. In Figure 2E, we show, for the first neuron, that the number of asynchronous SSEs for P600 was larger than the number of SSEs for P220, resulting in higher firing rates (turquoise vs. blue). In contrast, the number of synchronous SSEs was more significant for P220 than for P600 (red vs. pink). The same applied to the second neuron. The number of asynchronous SSEs for P600 is larger than the number of SSEs for P220, resulting in higher firing rates (turquoise vs. blue). In contrast, the number of synchronous SSE is more significant for P220 than for P600 (red vs. pink). Thus, in this example, these neurons preferred P600 with respect to their firing rates and P220 with respect to their degree of synchrony.

We calculated several relationships to quantify the transformation of whisker vibrations into neuronal discharges. First, we computed the Pearson correlation coefficient (for each neuron, for each trial) between low- and high-acceleration event ratios (Fig. 1H) and the firing rates and found it to be low (0.36 ± 0.18; Fig. 2F orange bar). Second, we calculated the correlation coefficient between the number of asynchronous SSEs and firing rates and found it to be relatively high (0.86 ± 0.05; Fig. 2F blue bar). Third, we calculated the correlation between the number of synchronized SSEs and SR values and found it to be 0.78 ± 0.18. These results suggest that neuronal firing rates cannot be accounted for by the proportion of high-magnitude SSEs. Moreover, the different aspects of neuronal responses vary differentially as a function of surface coarseness.

***Texture-dependent local coding***

Interactions between the whiskers and the environment lead to frictional movement and induce whisker bending, vibrations, and brief, discrete micromotions known as SSEs [[13](#_ENREF_13), [18-23](#_ENREF_18)][18-2318-2318-2318-2318-23](#_ENREF_18). Here we examined whether surface coarseness impacts the transformation of SSEs into neuronal discharges. An example of whisker motion across P220 and P600 sandpapers is shown in Figure 3A, revealing multiple brief, high-acceleration events during whisker motion. We next examined the role of synchronous vs. asynchronous spikes in tactile transformation. All coincident spikes occurring within the significant temporal window determined by the CCH width (See methods section) were designated synchronous and colored red, while all other spikes were designated asynchronous and colored black (Fig. 3A, upper panels). As can be seen from the trace, the synchronized spikes are interspersed with non-temporally correlated spikes. An examination of the neuronal response indicated that high-velocity events coincided with large negativities in the local field potential and the neuronal discharge. As we have shown previously [[56](#_ENREF_56)], each spike was driven by SSEs, and different aspects of these neuronal discharges convey information regarding the magnitude of an SSE. We calculated the STA of the synchronous and asynchronous spikes to examine whether these local transformations are different for synchronous and asynchronous spikes. As shown in Figure 3B, STAs calculated from the asynchronous spikes of these neurons (blue and red traces) were smaller and exhibited greater variance, whereas the STAs calculated from synchronous spikes (purple traces) were larger and had a lower level of variance.

To examine whether surface coarseness affects the transformation of SSEs into spikes, we investigated the relationship between SSE amplitudes in the different textures and various aspects of neuronal discharges. An example of this analysis for paired neuronal recording is shown in Figure 3C-D. First, we examined the relationship between the SSE amplitudes and the discharge probability in the two types of spikes. For this analysis, an SSE was defined as any peak that crossed a defined threshold (stick versus slip events were not distinguished; see Methods section). The analysis was confined to the initial 20 msec following each SSE. The net spiking probability of the asynchronous spikes increased gradually with increasing thresholds, indicating that these spikes can robustly convey the magnitude of SSEs based on their discharge probability (for example, for P600 and P220; Fig. 4C; a sigmoidal function fits these relationships). In contrast, the synchronous spikes exhibited almost an all-or-none behavior once they reached the higher threshold.

To quantify the differences between asynchronous and synchronous spikes for the different textures in all neurons, we calculated the mean and SD values of the slopes and the shifts in these curves. We found that asynchronous spikes changed their discharge probability as a function of SSE amplitude, as indicated by the smaller slope values. In contrast, the synchronous spikes rose sharply with SSE amplitude. Increasing surface coarseness resulted in an increase in the slope for asynchronous spikes as well as a rightward shift in the asynchronous and synchronous spike curves (Fig. 3E), with 0.85 and 0.97 representing the proportions of significant neurons manifesting this correlation for asynchronous and synchronized spikes, respectively.

Second, we investigated the relationship between SSE amplitudes and the neuronal discharge rates in the two groups of spikes, calculating firing rates over 30 ms (see Methods section). We detected a linear relationship between the neuronal discharge rates and the SSE amplitude for the asynchronous spikes (Fig. 3D). Comparing all neurons revealed that the asynchronous spikes conveyed the SSE amplitude through their firing rates, whereas the synchronous spikes did so poorly, with 98% and 5% of asynchronous and synchronous neurons exhibiting this phenomenon, respectively. Increasing surface coarseness resulted in an increase in the slope for asynchronous spikes and a rightward shift in the asynchronous spike curve (Fig. 3E). Together, these results indicate that surface coarseness affects the local transformation of SSE amplitudes into discharge probabilities and firing rates.

In a previous study [[56](#_ENREF_56)], we showed that the response latency for synchronous spikes, defined as the relative interval between network activity and spikes, and the relative spike timing between synchronous spikes depend on SSE amplitude. Here, we examined whether these response characteristics are influenced by surface coarseness. First, we calculated the relationship between SSE amplitude and spike latency. We examined synchronous spikes that show this dependency and compared this dependence across different textures. For each spike, we detected its underlying SSEs and quantified the timing of each SSE by defining the peak value that crossed the threshold at the mean±3 SD (Fig. 4A). The examples shown in Figure 4 are for the same neurons as in Figure 3. Figure 4B shows the dependence of synchronized spike latency on SSE amplitude for two textures. Each point represents an average of multiple points. These figures show that the spike latency in synchronous spikes was linearly dependent on the SSE amplitude. We then quantified this relationship by calculating the normalized slopes for all neurons with synchronous spikes for these textures, normalizing SSE slopes to the z score. We found that the synchronous spikes showed a significant latency dependence on the SSE position amplitude in 89% of the neurons (Fig. 5G, right panel).

Second, we examined the influence of SSE amplitude on the time interval between the sensory-evoked commencement of the LFP and associated spikes. We calculated its second derivative to define the sensory-evoked LFP starting point (Fig. 4C; See Methods section). We examined synchronous spikes that exhibited this dependency and compared such dependence across different textures. Figure 4D shows the dependence of the LFP-spike latency on SSEs amplitude for two textures in synchronous spikes. These results demonstrate that the LFP-spike latency for synchronous spikes was dependent on the SSE amplitude. We found that the synchronous spikes exhibited a significant latency dependence on the SSE position amplitude in 80% of the neurons (Fig. 4H).

Finally, we examined the influence of the SSE amplitude on the degree of spike synchrony, consistent with the inter-neuronal ISI (Fig. 4E; See Methods section). An example of this influence is shown in Figure 4F, demonstrating that a larger SSE amplitude resulted in a smaller ISI. This dependence could be fitted by an exponential decay function (Fig. 4F). These data show the dependence of ISI on SSE amplitude and highlight a decrease in this slope for coarser surfaces (Fig. 4I), with 90.2% of neurons exhibiting this significant dependence. This suggests that the particular aspects of asynchronous and synchronous spike responses are differentially affected by surface coarseness.

***Comparisons of the different coding strategies***

Figure 5 shows an example of the different coding strategies as a function of surface coarseness. Here we recorded from a pair of neurons shown in Figures 3-4, presenting the firing rate of each neuron (Fig. 5A; red and blue traces) and their synchronous activity (SR values; purple trace) as a function of surface coarseness. These results indicated that the first neuron exhibited a preference for the P600 texture whereas the second neuron exhibited a P220 preference. The synchronous activity of the two neurons also presented with a P600 preference. For the same neurons, Figure 5B shows the dependence of the local asynchronous number of spikes and probability slope on surface coarseness. These two response characteristics exhibited a preference for P600. Finally, Figure 5C highlights the dependence of local synchronous response characteristics on surface coarseness, specifically a preference for the P220 texture. Our results thus suggest that changes in texture coarseness lead to complex neuronal responses (Figs. 1-5**)**, which implies that cortical neurons may be selective for specific textures through a phenomenon termed texture selectivity [[72](#_ENREF_72)]. Notably, distinct coding strategies may present different texture selectivity.

We next examined several surface coarseness-dependent responses to compare three different coding strategies: selectivity, clustering, and similarity. Cortical neuron texture selectivity was assessed by using a texture selectivity index (SI) as a measure (Fig. 6A, B; see Methods section). First, we calculated the average firing rate across 75 trials for four different textures and computed the SI to quantify the statistical significance of texture selectivity. Second, we shuffled the firing rate of 75 trials between four textures 500 times and calculated the SI for each shuffling. Then, we calculated the mean+3SD for the 500 points of the SI data distribution (Fig 6B). If the calculated SI of the original data is higher than the shuffled SI (mean+3SD), the SI was considered statistically significant. We previously reported that more than 80% of the recorded cortical neurons are texture selective [[72](#_ENREF_72)].

When we plotted the firing rate and SR associated with the different textures of paired neurons (Figs. 1-6), we did not observe a linear relationship between the firing rate and SR with texture coarseness. This suggests texture preference for firing rate, temporal synchronization, and local characteristics (the mean value across all local features). To quantify these complex relationships, we divided the neural responses as a function of surface coarseness into four categories (Fig. 6C lower panels): 1. Up - neurons presenting a significant monotonic increase; 2. Down - neurons presenting a significant monotonic decrease; 3. Tuned - neurons exhibiting a preference for a specific texture; 4. No change - neurons that did not show any significant changes. This analysis revealed that most neurons show texture selectivity (Fig. 6C, middle panel) (0.82, 0.68, and 0.89 for firing rate, temporal synchronization, and local features, respectively). These results suggest that ~80% of the cortical neurons preferred a specific texture in global and local features. We divided these neurons according to their preferred texture and found neurons that preferentially responded to each of the examined textures (Fig. 6D). These results indicate that cortical neurons can represent a large range of surface coarseness.

To further examine texture selectivity, we calculated the texture SI for all coding strategies (Fig. 6E). We measured respective SI values of 0.35±0.19, 0.56±0.18, and 0.52±0.12 (mean ± SD, P<0.01) for the firing rate, synchronization, and local features, respectively. Thus, synchronous activity and local features show higher selectivity than firing rates. Finally, to examine the capacity of the different coding strategies to discriminate between the various surfaces, we calculated the ROC-based AUC values for all textures. The result indicated a significantly higher mean AUC value for local features (0.78) as compared to synchronization (0.61) and firing rate (0.57) (Fig. 6F). Together, these results suggest that the different coding strategies vary in their texture selectivity and ability to discriminate between textures.

We additionally assessed the similarity between the different coding strategies to determine whether different coding strategies exhibit the same surface coarseness preference. We divided the neurons into three categories: (1) Similar - different coding strategies show similar dependence on surface coarseness. In the case of firing rates and synchrony, the preferred texture firing rates for two neurons correspond to the preferred texture for synchronous activity (Fig. 7A); (2) Partially different - different coding strategies show partially similar dependence on surface coarseness. Only one neuron's preferred texture firing rates correspond to the preferred texture for synchronous activity (Fig. 7B); (3) Different - different coding strategies show dissimilar dependence on surface coarseness. None of the neurons' preferred texture firing rates correspond to the preferred texture for synchronous activity (Fig. 7C). Initially, we determined the preferred texture for each coding strategy (Fig. 6). Based on the similarity in surface coarseness preferences, we then divided the analyzed neurons into these three categories. For each group, we calculated Pearson correlation coefficient values between the plots, revealing that the proportions of cortical neurons in each of these categories for the relationship between firing rates and synchrony were: Similar - 0.2 (0.5), Partially different - 0.35 (0.56), and Different - 0.55 (-0.45) (Fig. 7D), where the values in parentheses are the average Pearson correlation coefficients among the different plots. We found the following distribution for the relationship between firing rates and local features: Similar - 0.1 (0.35), Partially different - 0.38 (0.58), and Different - 0.52 (-0.01). We repeated this analysis for the relationship between synchrony and local features, yielding the following group proportions: Similar - 0, Partially different - 0.25 (0.66), and Different - 0.75 (0.1). These results suggest that each of the three coding strategies embodies independent representations of surface coarseness for the same neurons.

Finally, a previous imaging study has shown that the cortical neurons cluster spatially following their texture selectivity [[72](#_ENREF_72)]. To examine the degree of spatial clustering of texture selectivity of neurons recorded from the same site (<150 µm), we devised a measure of similarity between adjacent neurons, termed the *cluster value*. We calculated this cluster value as the number of neurons selective to the same texture divided by the number of neurons in a particular cluster. A cluster value closer to 1 indicates that all neurons in the cluster have the same preferred texture. We found that for firing rates, the cluster value was 0.72±0.21, which was well above the significance level of 0.49 (see Methods section for details regarding the calculation of the significance level), indicating a high degree of texture similarity between adjacent neurons (Fig. 7E, blue bar). In several cases (*n* = 25), when we recorded from synchronous triplet and quadruplet neurons, we calculated the cluster value for synchronous neurons and found that this cluster value was 0.52±0.15, indicating a low degree of texture similarity between adjacent neurons (Fig. 7E, purple bar). We repeated the same analysis with local coding and measured a mean cluster value of 0.58±0.07 across all local features, suggesting that local features of neurons do not show spatial clustering. These results suggest a difference in the spatial organization of these three coding strategies.

### Discussion

In the current study, we explored the transformation of tactile inputs into cortical neuronal discharges by monitoring the kinematic and kinetic characteristics associated with whisker motion across textured surfaces and concurrently recording from a small population of cortical neurons. SSEs are a prominent feature of whisker-surface interactions. Recent studies have shown that the kinematic profiles of SSEs carry textural information [[21](#_ENREF_21), [44](#_ENREF_44)] and are encoded by neurons on the ascending tactile pathway [[10](#_ENREF_10), [25](#_ENREF_25), [41](#_ENREF_41), [45-55](#_ENREF_45)]. The magnitude and frequency of these events were correlated with texture, with rougher sandpapers eliciting a larger amplitude of SSE position and forces, as well as an increase in their number (Fig. 1H) [[21](#_ENREF_21)], as compared to smoother surfaces (Fig. 1C-D)[[21](#_ENREF_21), [66](#_ENREF_66)]. These changes may result from the relationship between high- and low-acceleration events (Fig. 1H) [[21](#_ENREF_21)]. The association between SSE magnitude, forces, and texture may result from greater friction between whiskers and rougher surfaces. These changes reflected the global interaction between surfaces and whiskers. Changes in surface coarseness also resulted in a modification in local interactions between the whiskers and surfaces [[43](#_ENREF_43), [56](#_ENREF_56), [66](#_ENREF_66), [78](#_ENREF_78)]. Since SSEs constitute a significantfactor contributing to most spike generation in vS1 neurons [[13](#_ENREF_13), [21](#_ENREF_21), [25](#_ENREF_25), [29](#_ENREF_29)] during whiskers-surface interactions (Figs. 3-4), it was hypothesized that the variations in the characteristics of SSEs as a function of surface coarseness are directly related to the mean neuronal firing rates (Fig. 1). However, these changes in whisker surface interactions, shown here and elsewhere to be gradual and surface coarseness-dependent, could not explain cortical selective neuronal responses (Fig. 1). We found that surface coarseness is encoded in the mean firing rate of vS1 neurons [[21](#_ENREF_21), [24](#_ENREF_24), [27](#_ENREF_27), [28](#_ENREF_28)]. These relationships indicate that most vS1 neurons exhibit a surface coarseness preference (Figs. 1, 5)[[72](#_ENREF_72)].

We have demonstrated that the magnitude and number of SSEs are components of the kinetic signature associated with various textures. However, the coding of these parameters by vS1 neurons is not a result of the direct transformation of whisker-surface interactions (Fig 2F, orange bar). Rather, texture-specific changes in firing rate depend on neural sensitivity to SSE kinetic and kinematic characteristics [[56](#_ENREF_56), [72](#_ENREF_72)]. Moreover, the direct relationship between SSEs and spike discharges argues against the notion that cortical neuronal discharges result from the temporal integration of the vibrotactile signal within relatively extended ranges. Thus, our results do not support a model in which surface coarseness is transformed into the mean firing rate of vS1 neurons [[21](#_ENREF_21), [24](#_ENREF_24), [27](#_ENREF_27), [28](#_ENREF_28)], indicating that it is related to the mean speed or total power of surface-induced whisker vibrations [[24-26](#_ENREF_24)].

Another novel and plausible coding strategy outlined in the current study relies on precise spike timing through the spatiotemporal synchronization of neuronal assemblies. We found that neuronal synchronization with millisecond precision is a prevalent and robust feature of both spontaneous and stimulus-evoked activity [[38](#_ENREF_38), [39](#_ENREF_39)]. We found that the tactile stimulus-driven neuronal discharge of nearby neurons consists of a mixture of synchronous and asynchronous spikes. This temporal synchronization is stimulus-driven [[56](#_ENREF_56)]. We further uncovered novel evidence that the degree of synchronization changes as a function of surface coarseness (Figs. 2A-C). These changes show a form of surface coarseness preference that manifests in these firing rates. Although this measure of neuronal synchrony is indicative of local temporal interactions, the SR value we used here reflects the ratio between the number of events resulting in synchronous spikes and that expected by chance. Thus, one may argue that this measure reflects global coding (Figs. 2E-F, blue and red bars) and may be attributable to variations in the number and magnitude of SSEs.

By measuring concurrent neuronal activity and whisker movement in response to multiple surfaces, we found that variations in surface coarseness resulted in changes in SSE characteristics. These changes, designated here as local changes, reflect the complex local transformation of the kinetic and kinematic characteristics of SSEs to yield neuronal discharges (Figs. 4-5). These surface coarseness-dependent changes were expressed in the distribution of SSEs underlying spike discharges. Changes in surface coarseness resulted in a shift in the amplitude of spike-generating SSEs (Fig. 1G, I; Fig. 2E). We were able to monitor the degree of synchrony between adjacent neurons and found that the neuronal responses to textures were composed of intermingled synchronous and asynchronous spikes (Fig. 2E) [[56](#_ENREF_56)]. Once we separated the synchronous and asynchronous spikes, we differentiated their underlying SSEs and successfully identified coexisting tactile information streams and corresponding coding strategies [[79](#_ENREF_79)]. Within a short time frame, asynchronous and synchronous spikes convey an unexpected level of detail regarding SSE magnitude via multiple channels, including spike rates and probability in asynchronous spikes (Figs. 3-4). Furthermore, synchronous spikes convey SSE magnitude through the precise timing of spikes between and within neurons (Fig. 4). Our data thus indicate that the relationship between SSE magnitude and the different features of neuronal responses can serve to discriminate between different textures (Figs. 4-5).

We have shown that most neurons exhibit a surface coarseness preference across all coding strategies (Fig. 6C) and that these neurons show a preference for all textures (Fig. 6D). By using AUC values and the selectivity index, we further determined that the tactile evidence carried by local coding was superior to other coding strategies with respect to discrimination among different textures (Figs. 6E, F). Moreover, comparisons of the specific preferred textures in the same neurons through these various coding strategies revealed that most neurons present with differing degrees of texture preference through these different coding strategies (Figs. 7A-D). Our findings indicate that the discrepancy between these coding strategies in transmitting preferred texture information thus stems from their sensitivity to different tactile features.

Whisker-surface interactions are likely to be modulated in response to environmental conditions, tasks, the motivation of the animal [[22](#_ENREF_22), [80-88](#_ENREF_80)], as well as considerable variations in stimulus configuration, whisker velocity, head movements, and object distances [[9](#_ENREF_9), [11](#_ENREF_11), [12](#_ENREF_12), [21](#_ENREF_21), [24](#_ENREF_24), [88](#_ENREF_88), [89](#_ENREF_89)]. These changes can lead to considerable changes in sensory signals [[90-92](#_ENREF_90)] and may differentially influence the various coding strategies, changing associated surface coarseness preferences.

These results suggest that cortical neurons may have access to a more detailed, dynamic description of tactile inputs than initially assumed. These coding strategies may enable spike trains to convey stimulus information through multiple complementary channels, each corresponding to a different aspect of the tactile world and its variations, thereby better coping with a dynamic and complex tactile environment.

*Methodological Considerations*

To explore the transformation of the tactile features of whisker vibrations into cortical neuronal activity, we used receptive sensing in which the whiskers are stationary and the surfaces move. Rats actively sweep their whiskers across surfaces to locate and distinguish objects in the animals’ immediate sensory environment [[8](#_ENREF_8), [93-97](#_ENREF_93)]. In addition, active whisking is often associated with head and body movements [[2](#_ENREF_2), [44](#_ENREF_44), [98-100](#_ENREF_98)]. Moreover, rodents often forego whisking, relying solely on passive movement of their whiskers instigated by body and head movements. Specifically, they use their vibrissae but do not whisk as they maintain contact with walls and surfaces while running.

The behavioral paradigms used to study texture discrimination extensively influence how rats use their whiskers to sense the tactile environment. In head-fixed animals, the only way to sense the surfaces is to whisk against them. However, to our knowledge, a quantitative examination has yet to be published regarding the influence of whisking strategies on texture discrimination under these conditions. That may be due to stable conditions in which the surfaces are located at a constant location and distance, influencing whisking strategies and making perception and discrimination less complex [[10](#_ENREF_10), [21](#_ENREF_21)].

In free-behaving animals, it has been shown that they develop a purposive whisking strategy for whisker-surface interactions that is information-seeking to perceive and discriminate between different textures. Thus, whisking behavior is related mainly to the gathering of tactile information, whereas discrimination performance appears to be more closely related to the details of whisker–surface interactions [[22](#_ENREF_22), [101](#_ENREF_101)]. Finally, it has been shown recently that free-behaving rats can discriminate fine tactile patterns while running without whisking [[102](#_ENREF_102)].

The present study primarily examined the transformation of whisker-surface interactions into cortical neuronal activity. While we use anesthetized rats in receptive sensing mode, our results are similar to those in awake-behaving animals in many respects. The occurrence and magnitude of SSEs are encoded by time-locked spikes in vS1 ensembles, with texture-related sequences of SSEs encoded by multiple coding strategies constrained by the intrinsic dynamics of whisker circuits and synapses. The occurrence of discrete SSEs related to texture, observed here, suggests coexisting coding for texture during active sensation while awake.

*Texture Preference in Cortical Neurons*

A hallmark of the sensorimotor system is that tactile features are organized according to maps whereby the functional role of a neuron, and its tuning to stimulus properties, can be predicted by its location. In the somatosensory whisker system, several properties of tactile stimuli have been spatially identified. First, whisker somatotopy is perhaps the most prominent property of the whisker pathway organization [[103](#_ENREF_103), [104](#_ENREF_104)]. Additionally, a map of directional selectivity has been observed in anesthetized and awake rodents performing active sensing [[53](#_ENREF_53), [105](#_ENREF_105), [106](#_ENREF_106)]. Another spatial feature of whisker stimuli is the degree of correlated motion across multiple whiskers [[107](#_ENREF_107)]. In contrast, the distribution of response selectivity for whisker angle, curvature, kinematic features, and distance to a wall found clear evidence favoring a salt-and-pepper distribution of feature selectivity [[105](#_ENREF_105), [108](#_ENREF_108), [109](#_ENREF_109)]. Studies of selectivity to texture coarseness in rats, tested under electrical whisking conditions, found that neurons preferring the same texture tend to cluster together within the Barrel [[72](#_ENREF_72)]. In the current study, using receptive sensing, we support our previous finding that cortical neurons exhibit surface coarseness preference through different coding strategies (Fig. 6).

Cortical neurons display spatial clustering according to their preferred texture selectivity. However, this clustering is restricted to firing rates only. Examination of the spatial organization through the two other coding strategies revealed no spatial clustering (Fig. 7E). Thus, our findings suggest that surface coarseness preference is an inherent feature of tactile transformation. These transformations may reflect a unique combination of kinetic and kinematic features for each texture. These combinations manifest themselves through the different coding strategies in which firing rates primarily represent global parameters such as the number and magnitude of SSEs. Synchrony coding reflects the number and magnitude of SSEs that resulted in synchronized spikes. These results suggest a differential role for these different coding strategies in which each neuron participates in overlapping populations coding different attributes of whisker-mediated sensory signals [[110-113](#_ENREF_110)]. A comprehensive understanding of how neuronal networks are organized will thus need to consider how different neurons convey sensory and other relevant signals under different tactile and behavioral conditions.

Figure Legends

**Figure 1. The influence of changes in surface coarseness on whisker vibrations, neuronal discharge rates, and SSE amplitude.** (**A**) An overview of the experimental design, demonstrating that whiskers are placed in contact with a rotating cylinder covered with textured sandpaper. (**B**) An example of C3 whisker movements in response to P400 and P800 textures. The vertical line on the whisker vibration scale bar indicates the image measurement, and the horizontal line indicates the time in milliseconds. (**C**) The influence of texture coarseness on the SD of whisker vibration position (orange) and curvature (turquoise) for the whiskers in (B). Asterisks indicate statistically significant differences between the groups (P < 0.01). (**D**) The influence of texture coarseness on the SD of whisker vibration position (orange) and curvature (turquoise) for all recorded whiskers. All SD values were normalized to P120. Asterisks indicate statistically significant differences between groups (P < 0.01). (**E**) PSTHs of two neurons were recorded simultaneously. (**F**) The influence of texture grit size on neuronal firing rates of the neurons in (E). (**G**) Normalized distribution of all SSEs that resulted in spikes of the neurons in E. (**H**) Ratio of the number of high- to low-acceleration events as a function of surface coarseness. Data shown in (H) are from all recorded whiskers; error bars represent the standard error calculated across all whiskers. (**I**) The influence of texture grit size on mean SSE resulted in spikes of the neurons in (E).

**Figure 2. Neuronal synchronization as a function of surface coarseness.** (**A-B**) PSTHs and CCHs correspond to four different textures: P120, P220, P600, and P800. The vertical scale bar for PSTH shows the spike probability. In the PSTHs, the dashed vertical line indicates the starting point of the stimuli. The vertical scale bar of the CCHs shows the number of spikes at zero time lag. The black arrows indicate the time window of significant synchronous spikes. (**C**) The influence of surface coarseness on neuronal firing rates and neuronal synchronization for the neurons in (A). (**D**) Distribution of SR values in all neurons. The pink distribution shows the SR values below one. (**E**). Normalized distribution of SSE amplitudes for the neurons in A-B resulted in asynchronous (blue and turquoise) and synchronous (red and pink) spikes for two textures. (**F**) The correlation between the low- to high-acceleration events ratio and firing rates (orange), between firing rates and the number of asynchronous SSE (blue), and between SR values (degree of synchronization) and the number of synchronous SSE (red) in all neurons.

**Figure 3. Cortical neuronal responses to textures are composed of intermingled synchronous and asynchronous spikes.** (**A**) An example of whisker motion, LFP, and spike discharge in two neurons in response to the P220 texture. The spikes marked in red are synchronous. (**B**) STA of whisker motion and synchronous (middle panels) and asynchronous spikes (left and right panels). (**C**) The relationship between detection threshold and firing probability for the neurons in (B) and in Figure 2, in asynchronous and (pink and turquoise) and synchronous (red and blue) spikes for the two textures. This relationship fits a sigmoidal function. (**D**) The relationship between SSE amplitude and firing rates for asynchronous spikes for one of the neurons in (B) for P220 (red) and P600 (blue) textures. Lines indicate the results of a linear regression analysis. (**E**) Population statistics for asynchronous and synchronized spikes for the two textures. The slope of the fit line for the firing rates and probability for asynchronous spikes exhibited a significant change as a function of surface coarseness, whereas the slope of synchronous spikes did not change. The shift in the fits for both types of spikes exhibited a significant change as a function of surface coarseness. Asterisks indicate significant differences (P < 0.01).

**Figure 4. Coding of surface coarseness through local features**. (**A**) Spike latency from its underlying SSE (red arrow to vertical dashed line) for synchronous spikes. (**B**) The relationship between SSE amplitude and spike latency in synchronous spikes for the P220 and P600 textures (left and right panels, respectively). Each point in the graphs represents the mean. The line is the linear regression fit of the data. (**C**) Spike latency from its underlying LFP (red arrow to vertical dashed line) for synchronous spikes. The LFP commencement was determined by the second derivative of the LFP (turquoise traces; see Methods section). (**D**) The relationship between SSE amplitude and LFP-spike latency in synchronous spikes for P220 and P600 textures (left and right panels, respectively). The line is the linear regression fit of the data. (**E**) Interneuronal ISI (vertical dashed lines) from its underlying SSE (red arrow) for synchronous spikes. (**F**) The relationship between SSE amplitude and interneuronal ISI for synchronous spikes. The line is the exponential decay fit of the data. (**G**). Distribution of the normalized linear regression fit slopes for the relationships between SSE amplitude and spike latency for P220 (red) and P600 (blue) in all neurons (P < 0.01). (**H**) Distribution of the normalized linear regression fit slopes for the relationships between SSE amplitude and LFP-spike latency for P220 (red) and P600 (blue) in all neurons (P < 0.01). (**I**) Distribution of the normalized linear regression fit slopes for the relationships between SSE amplitude and synchronous spike interneuronal ISI for P220 (red) and P600 (blue) in all neurons (P < 0.01).

**Figure 5. The influence of surface coarseness on firing rates, synchrony, and local features**. (**A**) The influence of surface coarseness (for neurons from Figs. 3-4) on neuronal firing rates in paired recordings (red and blue) and neuronal synchronization (purple). (**B**) Asynchronous spike local features (number of spikes (blue) and probability (black)). (**C**) Synchronous spike local features (first spike latency (orange), LFP-first spike latency (turquoise), and ISI (blue)).

**Fig. 6. Neuronal selectivity and discrimination**. (**A**) Quantification of texture selectivity. The plot compares the normalized firing rate for the different textures. Three different numerical values present the SI corresponding to these three conditions. (**B**) Average firing rate (75 trials) associated with textures P120, P220, P400, and P800.The SI value was 0.4751 (calculated using the formula in the Methods section). The inset shows the statistical significance of texture selectivity. The histogram shows the distribution of 500 SI values. The red and turquoise vertical lines represent the mean and mean+3SD of the SI data distribution, respectively. The mean+3SD of the SI data distribution was 0.19. (**C**) Four different groups of neurons based on the relationship between surface coarseness and neuronal responses (up, down, tuned, and no change; lower panels; see text). Neuronal firing rates (blue), synchrony (purple), and local features (turquoise) show that most of the neurons in the different coding strategies are tuned to a specific texture. (**D**) The coarseness preferring neuronal population was further subdivided according to their texture coarseness preference. (**E**) Mean selectivity index values for neuronal firing rates, synchronization, and local features. The error bars represent the SD of SI. Asterisks indicate significant differences (P < 0.01). (**F**) The mean AUC values for neuronal firing rates (blue), synchronization (purple), and local features (turquoise) across all textures in all neurons. Error bars represent the SD. Asterisks indicate significant differences (P < 0.01).

**Figure 7.** **Surface coarseness preferences in the different coding strategies**. (**A-C**) The different similarity categories: (**A**) Similar – all coding strategies show the same preference. (**B**) Partially similar - some coding strategies show the same preference. (**C**) Different – none of the coding strategies show the same preference. (**D**) Proportions of neurons in the different categories. (**E**) Mean spatial clustering values in the different coding strategies. The dashed horizontal line indicates the significance level (see text). Asterisks indicate significant differences (P < 0.01).

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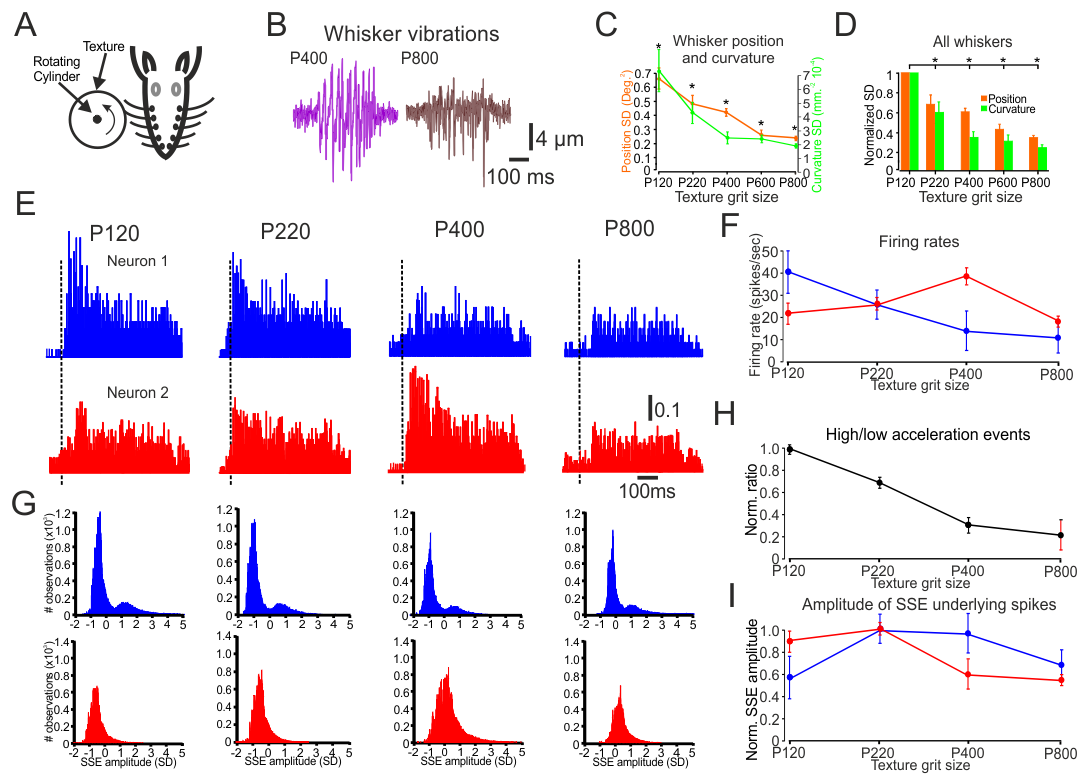
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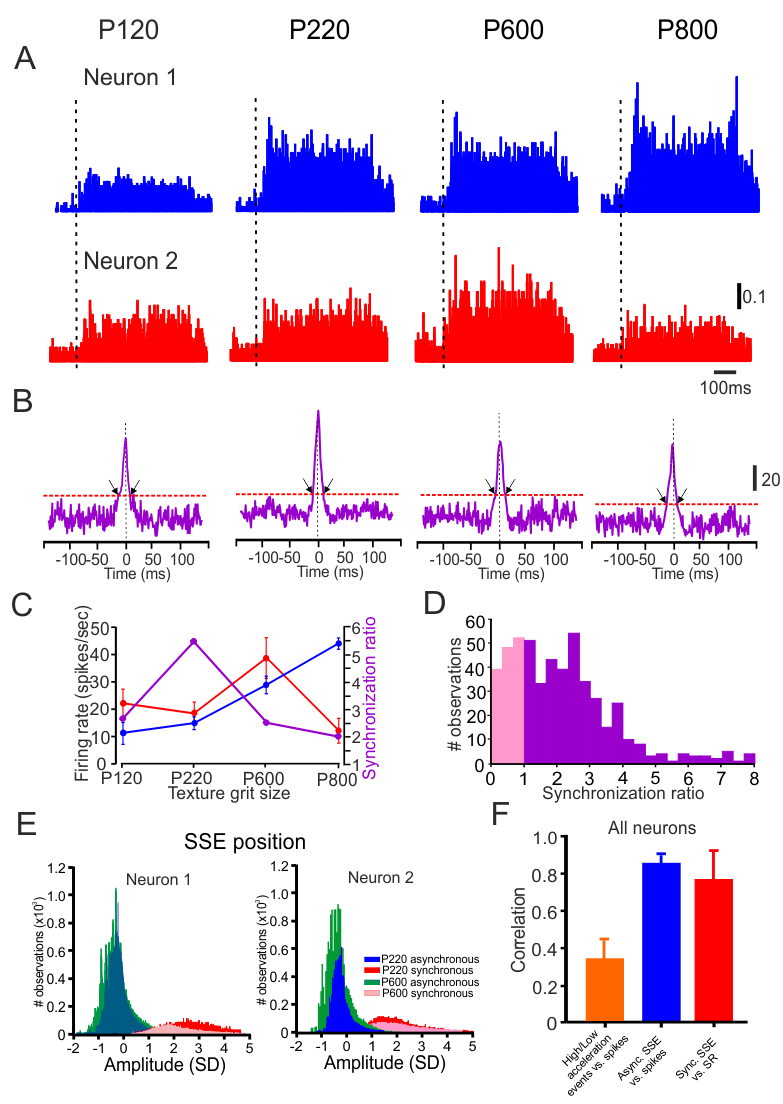
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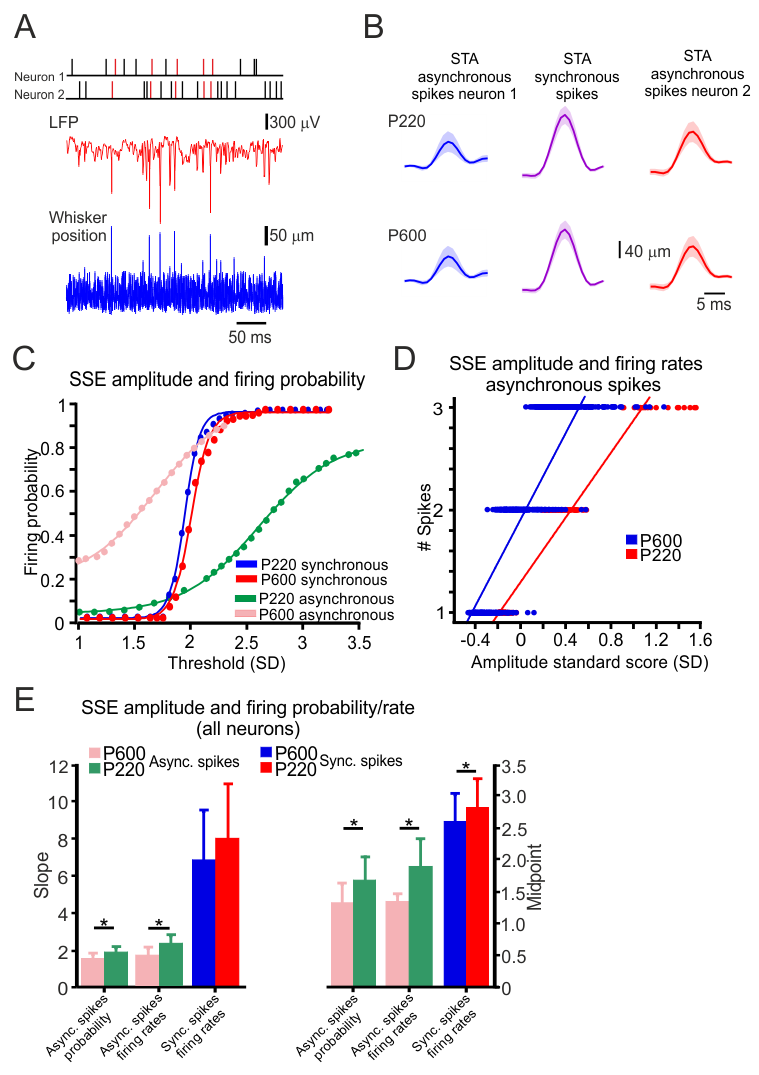
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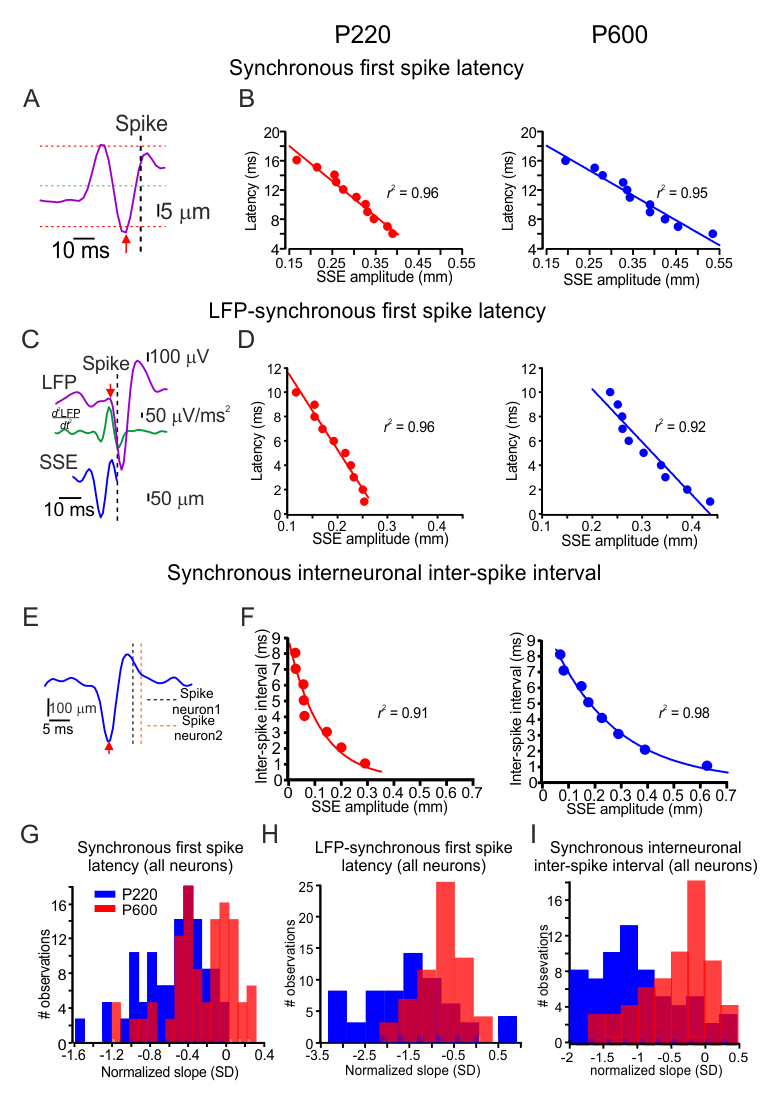
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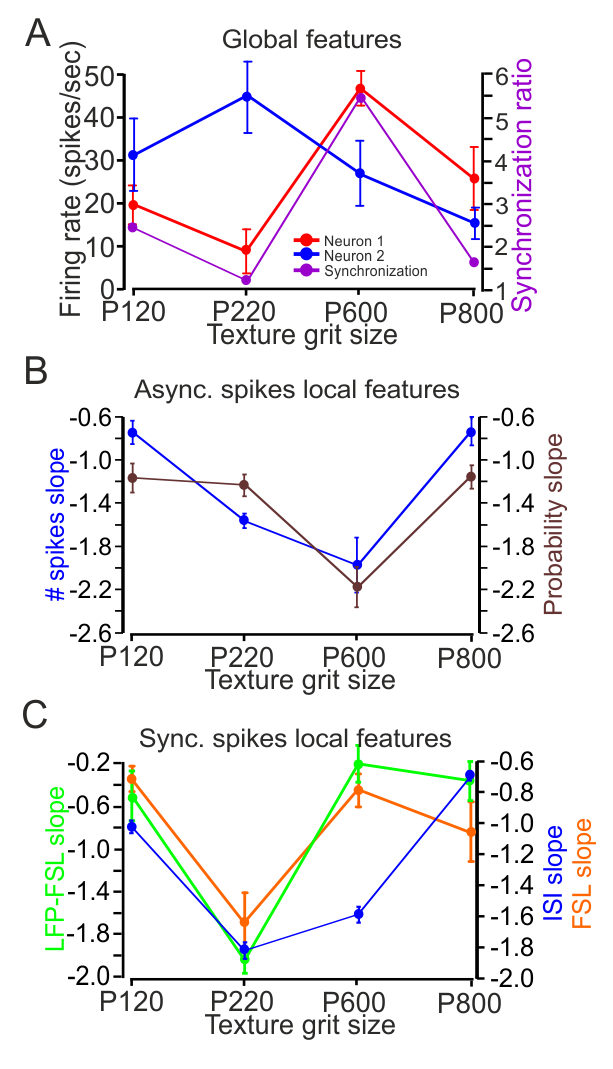
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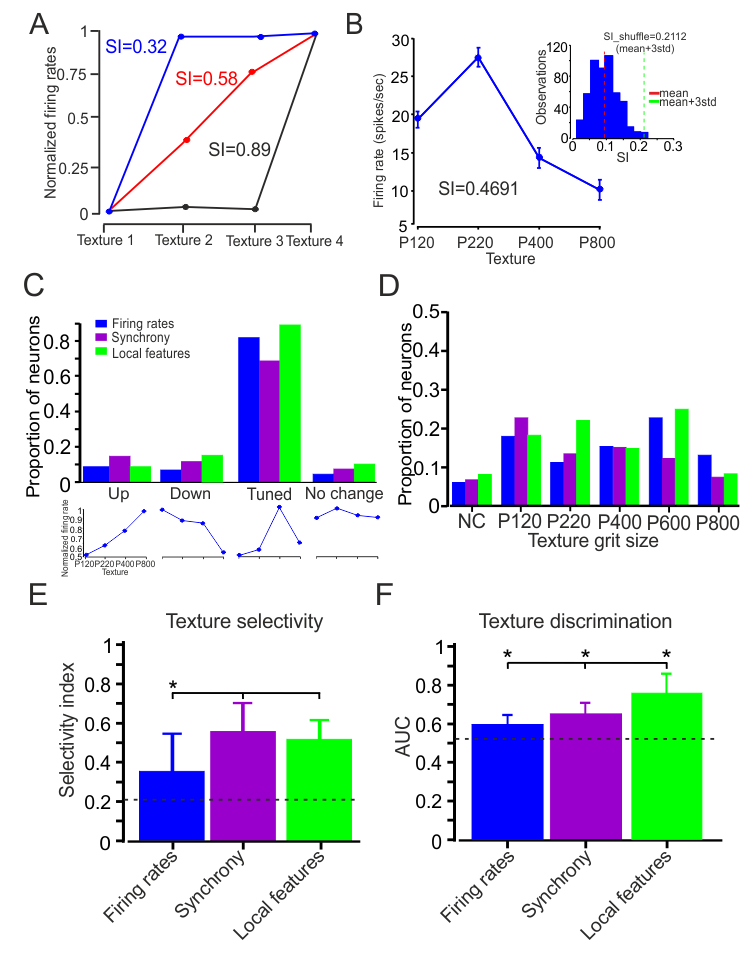
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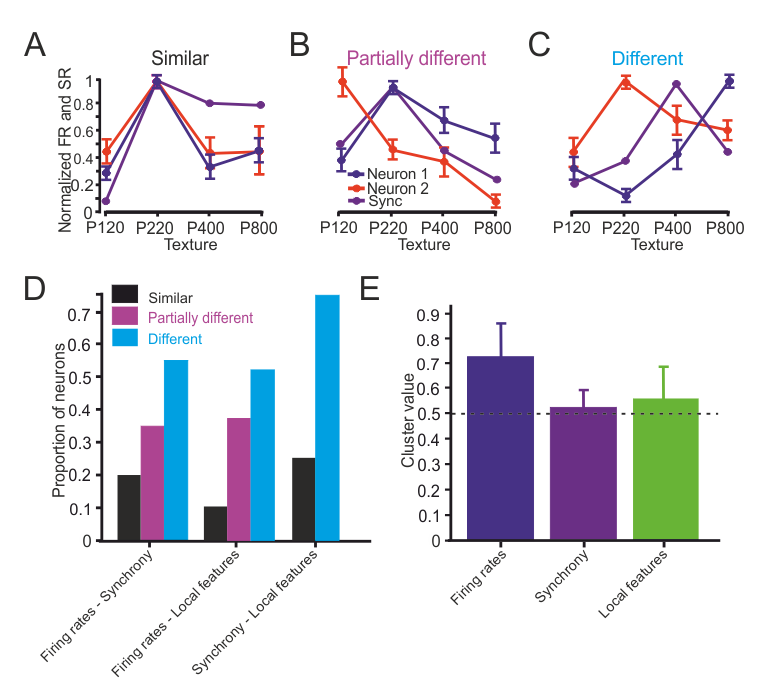
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