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Oscillatory activity of single units in a somatosensory cortex of an awake monkey and their possible role in texture analysis

(tactile sensation/phase-locked loop/corticothalamic loop/pattern recognition)

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ABSTRACT **Neuronal activity was extracellularly recorded in the cortex of an awake monkey (*Macaca fascicularis*). Single units displaying oscillatory firing patterns were found in the upper bank of the lateral sulcus in a region where most of the neurons responded to somatosensory stimuli. The spectral energies of the oscillating activity were distributed in a trimodal fashion—0–15, 15–50, and 80–250 Hz—with the most common frequencies around 30 Hz. The oscillatory activity was not affected by anesthesia, but it was often reduced by tactile stimulation or self-initiated movements. Analysis of the spike trains suggests that the majority of oscillatory activity was intrinsically generated by the neurons. A neural model of texture analysis is offered based on a corticothalamic phase-locked loop. The newly identified oscillators play a key role in this model. The relevance of the model to physiological, anatomical, and psychophysical data, as well as testable predictions, are discussed.**

Neurons throughout the ascending tactile sensory pathways preserve information on the phase of periodic stimuli (1–4). However, the central mechanism that "measures" the dominant interspike period of input trains has yet to be determined (1). One possible algorithm is a phase-locked loop (PLL), which compares the input period to the period of a local oscillator (5). A neuronal network capable of acting as a PLL would require intrinsic oscillatory activity in the same frequency ranges as its input.

Tactile input is mediated mainly by three subsystems, each most sensitive to a specific frequency range (1–3, 6): the slowly adapting (SA), the rapidly adapting (RA), and the pacinian (PC). There are several reports of single neurons with periodic firing patterns in the RA range (20–50 Hz) in subcortical somatosensory areas (7, 8). *In vitro* studies have shown the ability of neurons from the somatosensory cortex to oscillate in the same frequency range (9). In the awake animal, oscillatory activity (13–25 Hz) was detected in the electrocorticogram (10). Oscillations (25–85 Hz) were also found in the activity of small groups of neurons in the visual cortex of cats (11, 12). However, single-cell oscillators have not been reported yet in the somatosensory areas of the intact, awake animal, or in any other cortical areas.

We report here the finding of single cell oscillators in a somatosensory cortex of the intact awake monkey, and we suggest a role for these neurons in tactile processing, based on the PLL algorithm.

MATERIALS AND METHODS

A monkey (*Macaca fascicularis*; 5 kg) was trained to perform a simple reaction-time task. The monkey pressed a switch, which triggered short tone bursts; to gain a reward (a drop of juice), the monkey was required to release the switch as soon as the frequency of the tone changed. Once trained, the monkey was prepared for electrophysiological recording (13). A few days later, the recording sessions began. The activity of up to 11 single neurons could be recorded simultaneously by five microelectrodes with horizontal distances of 300–500 μm between their tips. Single units were recorded from both the upper bank (parietal opercula) and the lower bank (superior temporal plane) of the lateral sulcus.

The effects of auditory and somatosensory stimuli were examined. Auditory stimuli were presented during task performance. The stimuli consisted of 30-ms tone bursts or band-pass noise bursts at 70 dB (sound pressure level). Tactile stimuli were presented between blocks of task performance to examine the activity of selected neurons in the upper bank of the lateral sulcus. The stimuli (soft strokes or soft tapping) were manually applied to various skin areas. When a change in the firing rate or in the firing pattern of a neuron was observed, the same stimuli were applied repeatedly to the same skin area at a rate of one stimulus per second. At the end of the recording sessions the monkey was killed and the brain was prepared for histological observation (13). The somatosensory areas in the upper bank of the lateral sulcus were identified following previous descriptions (i.e., see ref. 14).

Autocorrelation histograms (ACH) and cross-correlation histograms (CCH) of all the recorded neurons were calculated and displayed on-line. Off-line analysis included in addition the examination of first-order time-interval histograms (TIH) and raster displays for all oscillating neurons. The data were then further analyzed by constructing ACHs and TIHs separately for four different time periods for the evaluation of the effect of stimuli (see *Results*).

RESULTS

Characteristics of Oscillatory Activity. The activity of 317 neurons was recorded at 65 different sites in an area of about 5 × 5 mm in the upper bank of the lateral sulcus. Histological observation and the physiological properties of the neurons indicated that the area was located at the posterior end of the somatosensory area II (14). Oscillatory firing patterns were detected in 43% of these neurons. In some cases, the oscillations were stable, lasting long periods; in other cases, the neuron switched from oscillatory to nonoscillatory firing patterns. Fig. 1 illustrates the firing patterns of an oscillatory neuron (Fig. 1*A*) and a nonoscillatory neuron (Fig. 1*B*) recorded simultaneously by one microelectrode.

Clear oscillatory firing patterns were detected in 74 neurons. All these neurons fulfilled the following criteria: (*i*) the

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Abbreviations: ACH, autocorrelation histogram; CCH, cross-correlation histogram; PC, pacinian; PD, phase detector; PLL, phase-locked loop; RA, rapidly adapting; SA, slowly adapting; RCO, rate-controlled oscillator; TIH, time-interval histogram; INH, inhibitory cortical neuron.

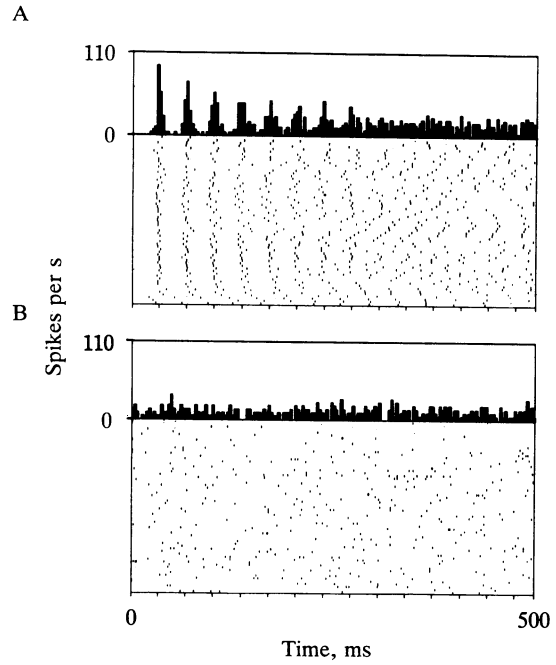

FIG. 1. Raster displays and ACHs illustrating oscillatory (*A*) and nonoscillatory (*B*) firing patterns of two neurons. Each line in the raster display starts when the neuron fired a spike. Occurrences of succeeding spikes of the same neuron during an interval of 500 ms are shown by the dots along the line. The solid histogram is the ACH computed for the spike train shown. The *y* axis of the ACH represents the firing rate (spikes/s) of the neuron as a function of time that elapsed since the neuron fired a spike at time 0.

ACH induced at least three peaks, with <15% jitter of the interpeak intervals; (*ii*) the modulation depth of the second peak exceeded 20% of the mean firing rate; and (*iii*) the second peak was significantly above chance level ($P < 0.01$). An additional 65 neurons showed weaker oscillatory patterns that did not meet all the above criteria. Examples of three different oscillation frequencies (7.2, 29, and 131 Hz) are illustrated by the ACHs in Fig. 2*A*. The distribution of

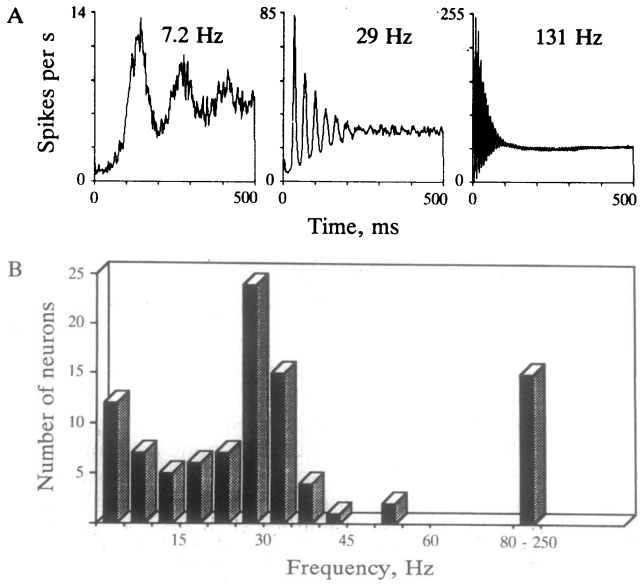

FIG. 2. (*A*) ACHs illustrating three oscillation frequencies of three different neurons. (*B*) Distribution of oscillation frequencies in the upper bank of the lateral sulcus. Data from 74 clearly oscillating neurons are included. Fifteen neurons had more than one oscillation frequency, in most cases within the same modality (10/15). Only three neurons had two or three frequencies simultaneously.

oscillating frequencies of the "clearly oscillating" neurons ($n = 74$) is shown in Fig. 2*B*. The distribution is nonuniform and includes three basic classes: 0–15, 15–45, and 80–250 Hz. The small number of high frequencies does not allow for determining whether the high-frequency range is unimodal.

It is important to mention that in the lower bank of the sulcus (the auditory cortex) where 831 neurons were recorded, only 14 weakly oscillating neurons (at 5–30 Hz) were found. The oscillatory activity appeared only for short periods and never met the above criteria.

Effect of Somatosensory Stimuli. Possible causes for the modification of firing patterns were explored by examining the activity of 38 oscillating neurons during different periods. Comparisons of the spontaneous activity to the activity when effective tactile stimuli were applied to the skin revealed that tactile stimuli completely suppressed the oscillations in all the tested neurons ($n = 11$). An example of the effect of two different tactile stimuli on the firing patterns of two simultaneously recorded neurons is shown in Fig. 3. Both neurons

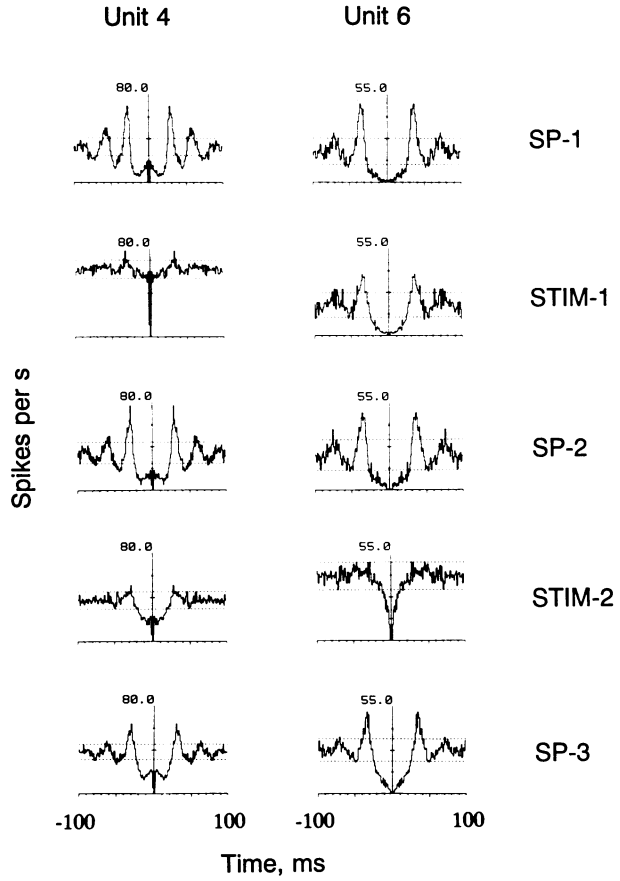

FIG. 3. ACHs illustrating the suppression of oscillatory activity as a result of tactile stimuli. (*Left*) Neuron 4 (33 Hz, full scale: 80 spike/s). (*Right*) Neuron 6 (27 Hz, full scale: 55 spike/s). Five consecutive periods are shown. SP-1, 131 s of spontaneous activity; the oscillatory activity is clearly seen. STIM-1, 147 s of soft strokes (1/s) to the contralateral small toes; the oscillations of unit 4 were suppressed and its average firing rate was elevated from 32 to 62 spikes/s; the firing rate of unit 6 was not affected and its oscillations were affected only very slightly. SP-2, 90 s of spontaneous activity; note the recovery of unit 4's oscillations. STIM-2, 117 s of soft strokes (1/s) to the contralateral big toe; the oscillations of the two neurons were suppressed; while the firing rate of unit 6 increased from 22 to 40 spikes per s, the firing rate of unit 4 was not affected. SP-3, 136 s of spontaneous activity; the oscillations recovered again. Recording of the two neurons lasted while the procedure (SP-1, STIM-1, SP-2, STIM-2, SP-3) was repeated seven times with similar results. In three sets, the procedure was carried out under ketalar anesthesia.

(units 4 and 6) showed clearly oscillatory patterns (SP-1 to -3), which were suppressed by tactile stimuli (STIM-1 and -2). The figure further illustrates that tactile stimuli had diverse effects on the mean firing rates and on the temporal firing patterns of the two neurons. Overall, we found no consistent relationship between a neuron's firing rate and the pattern of its oscillatory activity.

Comparisons of the activity during intertrial intervals of task performance (between the time of key release and the time of the subsequent key press) to the activity during the intratrial intervals (the time when the key was pressed) were made for 27 neurons. In almost all cases, the oscillatory firing pattern was either significantly decreased (n = 12) or completely suppressed (n = 10) during the intertrial intervals compared to the intratrial intervals. Four neurons had similar oscillatory activity during the two time periods, and only one neuron exhibited a stronger oscillatory firing pattern during the intertrial intervals.

During the intratrial interval, the monkey pressed the switch for 1–2 s. He was alert but relatively motionless and prepared to release the switch when the signal was given. During the intertrial interval, lasting 1–3 s, the monkey released the switch, received a reward, and was free to move his limbs until the next trial started. The suppression of oscillations, therefore, could result from a decrease in alertness or from an increase in the number of limb movements associated with uncontrolled somatosensory stimuli during the intertrial intervals.

To examine the possible effects of the animal's alertness on the oscillatory activity, we slightly anesthetized the monkey (by intramuscular injection of 0.5 mg of ketamine hydrochloride) during 12 sessions while recording oscillatory neurons. In all cases, the oscillation intensity of the neurons either showed no effect or increased slightly, yet the suppressive effect of tactile stimulation was maintained. We therefore conclude that the alertness level did not affect the oscillations, while tactile stimuli suppressed them.

Origin of the Oscillations. While determining the oscillations' origin definitively would require intracellular studies, the origin can be tentatively deduced from the neurons' spike-timing patterns. The distribution of intervals between successive spikes in an oscillatory spike train of a single neuron may be either unimodal (the fundamental interval alone appears with high probability) or multimodal.

A unimodal distribution emerges if the initiation of each oscillation cycle of a neuron depends on the firing of a spike by that neuron at the end of the previous cycle. This occurs when the oscillations are generated solely by intrinsic cellular mechanisms (15) or when the neuron is a member of a small oscillatory network of tightly coupled cells. A multimodal distribution emerges when the neuron is externally driven by both oscillating and nonoscillating sources, when the neuron participates in a large reverberatory circuit with loose connections between the cells, or when its firing is modulated by both subthreshold intrinsic oscillations and external influences. In all these cases, oscillatory activity depends on external drives. Due to noisy influences and low synaptic efficacy (16) the neuron may fail to fire at the time determined by the fundamental period, without disturbing the oscillatory pattern generator. In this case, multiples of the fundamental interval appear in the TIH (harmonic multimodal distribution). A multipeak TIH may also emerge when the neuron is driven by several oscillating sources of different frequencies (nonharmonic multimodal distribution).

TIHs were computed for all the clearly oscillating neurons; 66% of the neurons had unimodal TIHs, such as the one shown in Fig. 4*C*, while 31% had TIHs with more than one peak. These TIHs usually had two peaks and sometimes more (as in Fig. 4*D*, which shows at least three peaks). Only two neurons had nonharmonic multimodal TIHs.

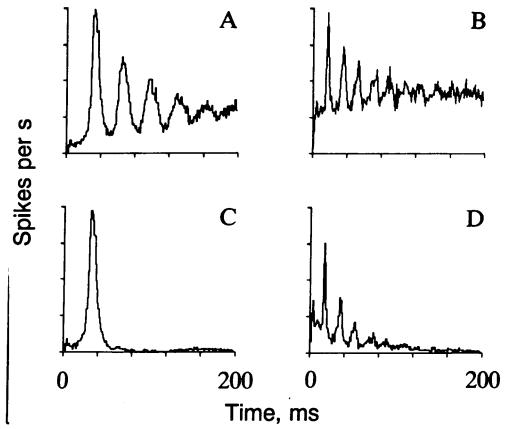

FIG. 4. Two oscillating neurons exhibiting the two types of TIHs that were observed. (*A* and *B*) The ACHs are shown. The oscillation frequencies were 31 and 55 Hz, respectively. (*C* and *D*) The corresponding TIHs are shown. (*C*) A unimodal TIH, indicating a highly regular firing rate with firing intervals confined mostly to one range, corresponding to the oscillation frequency. (*D*) A harmonic multimodal TIH, where multiples of the fundamental firing interval were present.

It was found that neurons with unimodal TIHs tended to exhibit more stable oscillatory firing. Most of these neurons had oscillatory activity >50% of the recording time, while all neurons with multipeak TIHs were oscillatory for <50% of the time. Based on our data, we hypothesized that the oscillations of a neuron with a unimodal TIH are locally generated by the neuron itself (or by a few tightly coupled neurons), while oscillations of a neuron with a multimodal TIH depend on external drives. We define the first type as a "local oscillator" and the second type as a "driven oscillator."

Cross-Correlation Analysis. The interactions between neurons were examined by performing cross-correlation analysis for all the simultaneously recorded pairs of neurons (343 pairs with at least one oscillating neuron, including 89 pairs in which both neurons were oscillating). The ACHs and CCHs of four simultaneously recorded neurons are shown in Fig. 5. Three of the neurons exhibited clear oscillations, yet there is no sign of correlation between any of the neuron pairs. We failed to detect statistically significant correlated oscillatory activity between any of the 343 tested pairs of neurons even when both oscillating neurons were recorded by a single microelectrode (25/89) or when they had very similar (±1%) oscillation frequencies (22/89). Similarly, no correlated oscillations could be found during periods of tactile stimulation.

The lack of strong interactions or correlated oscillatory activity indicates that the oscillations of different neurons were independent of each other, supporting the hypothesis that the majority of the neurons were independent local oscillators.

DISCUSSION

The cortical oscillators were found in a somatosensory area in the upper bank of the lateral sulcus of an awake monkey. The majority of the oscillating frequencies were confined to a range around 30 Hz. In the somatosensory cortex of awake monkeys, Rougeul *et al.* (10) described rhythmic activity (13–25 Hz) of the electrocorticogram that was blocked by body movement, similar to the effects that we described on the oscillatory activity of single neurons. In the somatosensory nuclei of the thalamus, Poggio and Viernstein (7) described periodic firing patterns of 20–30 Hz in the activity of single neurons. These oscillations were not suppressed by somatosensory stimuli, but their frequency could be modu-

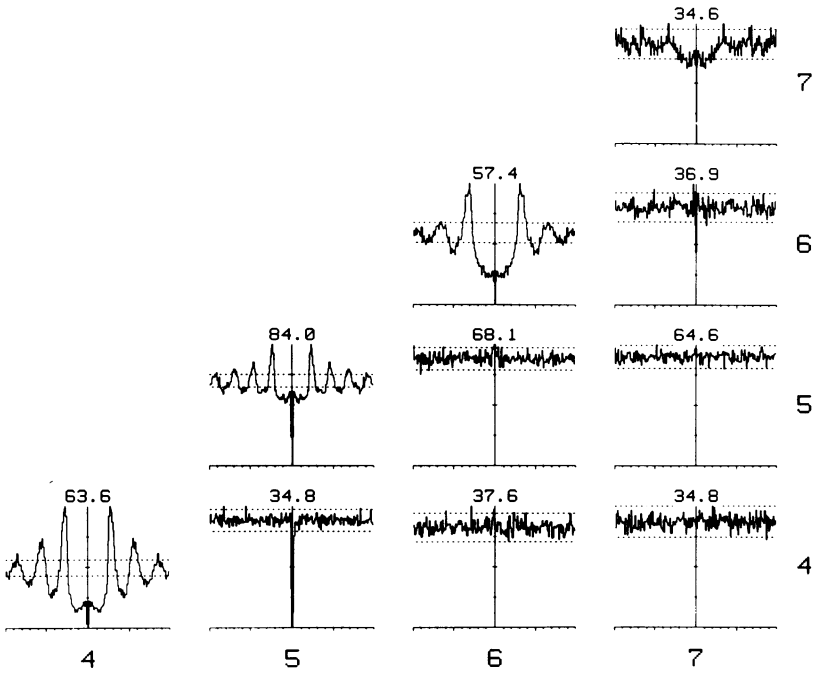

FIG. 5. An example of noncorrelated oscillatory activity of four neurons. Two neurons (neurons 4 and 5) were recorded by one microelectrode and the other two were recorded by another. ACHs are shown on the upper diagonal and the CCH for each pair is shown at the corresponding place in the matrix. The time span of each correlogram is ±100 ms. For each correlogram, the full scale (spikes per s) is shown above the *y* axis and a band of 99% confidence limits for the equivalent, independent Poisson processes is shown by the broken lines. Neurons 4, 5, and 6 were oscillating at frequencies of 34, 43, and 28 Hz, respectively. The CCHs between them are "flat," indicating that the three neurons were oscillating independently of each other.

lated. They suggested that the mean firing rate of a thalamic neuron and its oscillating frequency reflect different aspects of neural behavior. Our data (Fig. 3) suggest that this also holds true for cortical neurons.

Recently, oscillations of a similar frequency range were found in the activity of small neuronal groups in the cat visual cortex (11, 12). As opposed to the oscillatory activity of single neurons in the somatosensory cortex of the monkey, the visual oscillations were evoked by an effective stimuli and were clearly observed in the CCH. It is possible that these dissimilarities reflect merely the different species or alertness levels. It is more likely, however, that the differences reflect diverse functions of oscillatory activity in visual vs. somatosensory perception.

Several properties of the oscillating neurons in the somatosensory area strongly suggest that they participate in somatosensory processing: their firing rates and oscillatory components could be affected by tactile stimuli (Fig. 3), and the distribution of oscillating frequencies (Fig. 2) resembles the distribution of frequency tuning of the mechanoreceptors in the finger tip (1, 17, 18). Talbot *et al.* (1) compared response properties of mechanoreceptive fibers to the human ability to discriminate between vibratory stimuli of different frequencies. They suggested that "a central neural mechanism exists which alters its own activity (which 'measures') the dominant period in the input train of impulses." One possible mechanism to perform such a task is the PLL, an algorithm often used for decoding frequency-modulated signals. A PLL measures the dominant input period by comparing it to the intrinsic period of a local oscillator (5). Since the spatial frequencies of a texture are represented by temporal frequencies of the firing of mechanoreceptive fibers (2), a PLL could be used for texture decoding.

We have developed a PLL-based model for texture decoding, which will be described in detail elsewhere. The heart of the model is a set of corticothalamic loops that serve as PLLs (Fig. 6). Each PLL is composed of a thalamic phase detector (PD) and a cortical rate-controlled oscillator (RCO) arranged in a negative feedback loop (Fig. 6 *Upper*). The PD output is proportional to the phase difference between its two inputs. The oscillation frequency of the cortical RCO is modulated by the thalamic PD [mediated by inhibitory cortical neurons (INHs)]. Instantaneous changes in the input frequency are represented by the firing rate of a population of PD neurons. It can be shown mathematically that optimal detection is achieved when the input frequency to the PD is close to the RCO frequency. It is therefore suggested that PLLs are embedded in a circuit (Fig. 6 *Lower*) that controls the finger's traversing velocity so that the average spatial frequency of the surface is transformed to a temporal frequency equal to the intrinsic frequency of a selected set of local oscillators. For example, input from RA mechanoreceptors is best analyzed if the average input frequency is maintained near 30 Hz, implying that moving the finger across the surface at an appropriate velocity could improve texture discrimination. Indeed, it was reported that performance of a tactile discrimination task is optimized by allowing the subject to move his fingers across the target (19, 20).

Previous studies suggest that neuronal implementation of PLL-like circuits is plausible. The mechanoreceptors and their fibers filter and transform spatial frequencies of the surface to three classes of temporal frequencies of spikes (1–3, 6). The model requires a separation between channels of different frequencies. Indeed, tactile information is carried in three separate frequency channels (the three submodalities SA, RA, and PC) throughout the somatosensory pathways from the periphery to the cortex (21) and back to the thalamus (22). A substantial part of the thalamic input projects to inhibitory neurons in the cortex (23, 24). The structure of connections between the elements of the model was designed to match these properties of the somatosensory system. In fact, a thalamocortical loop of a similar structure has been proposed to exist in the mouse brain (24).

The local oscillators described here could serve as the local controllable oscillators of the model (RCO) and the driven oscillators could be related to, or affected by, the hypothetical PD neurons (like the INH of the model). Our finding that nonperiodic stimuli suppressed the oscillations corresponds to the prediction that RCO neurons track, at least to some extent, the input frequency; when the input is nonperiodic, the RCO losses its periodic firing pattern in an attempt to follow the input.

Several testable predictions stem from the model. (*i*) The local oscillators should track small variations in the frequency of vibratory stimulus around their spontaneous oscillating frequency. (*ii*) The delay between the stimulus and the spikes of the local oscillator should increase as the stimulus frequency is increased. (*iii*) Correlated activity

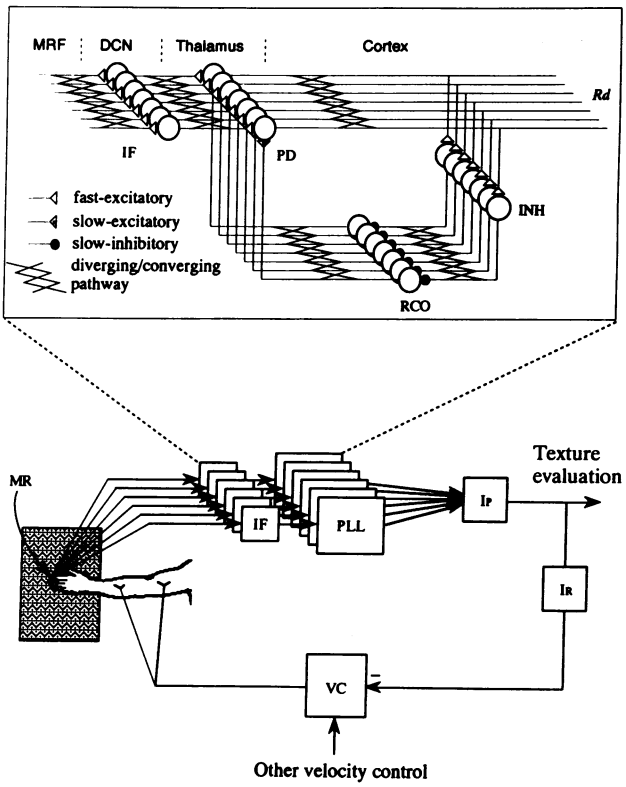

FIG. 6. A PLL model for texture decoding. (*Upper*) The structure of a single PLL circuit. The input from a set of mechanoreceptive fibers (MRF) is relayed by dorsal column nuclei neurons (DCN) to thalamic neurons, which serve as PDs. The number of parallel neurons in the loop was arbitrarily set at 7 for clarity. The MRF and DCN compose the input filter (IF). Rd is the instantaneous population firing rate of the PD neurons. The negative feedback loop is composed of thalamocortical connections between PD and INHs, local connections between INHs and RCOs, and corticothalamic projections from RCO neurons to PD neurons. (*Lower*) The structure of the full texture decoder, where a large number of PLLs (only six are shown) are arranged in parallel. They comprise the feedforward part of a negative feedback loop, which controls the finger's traversing velocity. The PLL output is integrated (by IP) to evaluate the texture and then low-pass filtered (by IR) to regulate the velocity controller (VC).

should be found between local and driven oscillators when vibratory stimuli of a frequency equal to the frequency of the local oscillator are applied. (*iv*) Texture perception should be optimized by controlling the finger velocity. That is, when a subject is asked to explore the texture of a surface, the finger's velocity should decrease as the average spatial frequency of the surface increases, so that the average temporal frequency of the input remains within a selected range. (*v*) Exploring velocities should be selected to maintain the average temporal frequency of the input equal to one of the three ranges of oscillating frequencies (Fig. 2), where the most common range, corresponding to the RA range (30 Hz), is preferred.

Whether the newly identified neuronal oscillators play a role in the central mechanism that detects and measures periodicity, and whether a PLL-like algorithm is used for this purpose in the brain, must be confirmed by future research in which these predictions are challenged.

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