Decoding stimulus features in primate somatosensory cortex during perceptual categorization

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Neurons of the primary somatosensory cortex (S1) respond as functions of frequency or amplitude of a vibrotactile stimulus. However, whether S1 neurons encode both frequency and amplitude of the vibrotactile stimulus or whether each sensory feature is encoded by separate populations of S1 neurons is not known. To further address these questions, we recorded S1 neurons while trained monkeys categorized only one sensory feature of the vibrotactile stimulus: frequency, amplitude, or duration. The results suggest a hierarchical encoding scheme in S1: from neurons that encode all of the sensory features of the vibrotactile stimulus to neurons that encode only one sensory feature. We hypothesize that the dynamic representation of each sensory feature in S1 might serve for further downstream processing that leads to the monkey’s psychophysical behavior observed in these tasks.

A vibrotactile stimulus is composed of both frequency and amplitude, indicating that there is dependency between the two sensory features. In principle, this dependency could be dissociated, by quantifying the psychophysical behavior and neuronal responses as functions of the stimulus amplitude while maintaining fixed the stimulus frequency and vice versa. For example, in a vibrotactile detection task, monkeys detected the stimulus amplitude and the recorded S1 neurons increased their firing rates as a function of the stimulus amplitude and correlated with the animal’s psychophysical performance (1). Also, in a vibrotactile discrimination task, monkeys discriminated the difference in frequency between two consecutive vibrotactile stimuli and the recorded S1 neurons increased their firing rates as a function of the stimulus frequency and correlated with the animal’s psychophysical performance (2). The question is: Do S1 neurons encode both stimulus amplitude and frequency of the vibrotactile stimulus, or is each stimulus feature encoded by separate populations of neurons?

Although this question appears simple to address, complexities arise. For example, recent studies have suggested that S1 neurons encode the mean velocity of the vibrotactile stimulus, which is the product of both stimulus amplitude and frequency (3). Also, in psychophysical experiments, humans reported changes in the perceived intensity of the stimulus as a function of amplitude or frequency (4), and the recorded S1 neurons in anesthetized rats indicated that their responses are associated with the mean velocity of the stimulus (5). These results show that there is an interaction between the two stimulus features and suggest that for a certain range of frequencies, it is almost impossible to distinguish between two stimulus frequencies when the intensities of the two stimuli are perceived of the same magnitude (6–8).

Therefore, we need further experiments in which S1 neurons are recorded when a subject performs a vibrotactile task as a function of the stimulus amplitude or as a function of the stimulus frequency. Such experiments could provide meaningful information on the encoding capacities of S1 neurons during these tasks. Also, it has been shown that the stimulus duration can bias discrimination performance, but it is not clear how this variable affects vibrotactile discrimination (9).

In this work, we show the encoding capacities of single S1 neurons while trained monkeys categorized only one sensory feature of the vibrotactile stimulus: frequency, amplitude, or duration. The results suggest a hierarchical encoding scheme in S1: from neurons that encode all of the sensory features of the vibrotactile stimulus to neurons that encode only one sensory feature. Furthermore, the S1 neurons that encoded each sensory feature correlated with the animals’ categorization behavior.

Results

Two monkeys (Macaca mulatta) were trained to perform a vibrotactile categorization task (Fig. 1). In separate blocks of trials, monkeys categorized one sensory feature of the mechanical vibration delivered to the glabrous skin of one fingertip of the right, restrained hand: frequency (Fig. 1A), amplitude (Fig. 1C), or duration (Fig. 1D). For example, in the case of frequency, monkeys first categorized two extreme stimulus frequencies, 10 and 30 Hz, and reported which was low or high, by pressing one of two push buttons (PBs) with the left free hand. We then presented a block of trials with frequencies ranging between 10 and 30 Hz (Fig. 1B; green plot). Monkeys then switched to categorization of frequencies ranging between 14 and 78 Hz (Fig. 1B; red plot), provided they first performed a few trials with the two new extreme frequencies, 14 and 78 Hz. This protocol was then followed when monkeys categorized the stimulus amplitude (Fig. 1C and D) or stimulus duration (Fig. 1E and F). The idea for using these stimulus sets is that the same sensory feature had to be classified as low or high (sets of frequency or amplitude) and short or long for the stimulus duration sets. Thus, depending on the stimulus configuration set, the monkey had to change the categorization rule. Another question that can be addressed in this task is: What is the relationship between the stimulus feature encoding in S1 and the animal’s categorization performance? It is important to emphasize that the stimulus amplitude (50 μm) and duration (300 ms) were maintained fixed during categorization of vibrotactile stimulus | psychometric functions | neurometric functions

Significance

A key step in studying perceptual categorization mechanisms is to understand how neurons from early sensory cortices encode the relevant features categorized of a sensory stimulus and how they relate to it. We studied the encoding capacities of primary somatosensory cortex (S1) neurons while trained monkeys categorized only one sensory feature of a vibrotactile stimulus: frequency, amplitude, or duration. The results suggest a hierarchical encoding scheme in S1: from neurons that encode all sensory features of the vibrotactile stimulus to neurons that encode only one sensory feature. Sensory feature encoding in S1 could serve downstream networks for constructing perceptual categorization.

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performed the task, the activity was recorded from single neurons in S1 (areas 1 and 3b) with stimulus delivered in the center of their cutaneous receptive fields. In the following sections, we show the responses of S1 neurons to each sensory feature of the vibrotactile stimulus and how they relate to the animal’s psychophysical categorization performance.

Responses of S1 Neurons During the Categorization of Vibrotactile Stimulus Features. Previous studies have shown that S1 neurons increase their firing rates as a function of the increasing stimulus frequency and that these responses account for the monkey's discrimination performance (2, 9, 10). However, the stimulus frequencies used in this task were in the flutter range only. In these studies, the stimulus amplitude was seven times the detection threshold, in such a way that monkeys based discrimination between frequencies and not on stimulus detection (2, 9, 10). Here, we studied the dynamic responses of S1 neurons (areas 3b and 1) in the flutter range (10–30 Hz; Fig. 2A) and with another stimulus set of frequencies ranging between the flutter and vibration (14–78 Hz; Fig. 2B) during the frequency categorization task. As shown in Fig. 2 C and D, this example S1 neuron increased its firing rate as a function of the increasing stimulus frequency. It is important to emphasize that all neurons tested (n = 147, stimulus set ranging from 10 to 30 Hz; n = 113, stimulus set ranging from 14 to 78 Hz) with these stimulus sets increased their firing rates as a function of the increasing stimulus frequency. Also, we found that both slowly adapting (SA; n = 50, 34% of the 147; n = 39, 34.5% of the 113) and quickly adapting (QA; n = 97, 66% of the 147; n = 74, 65.5% of the 113) S1 neurons responded similarly. Previous studies showed that few S1 neurons of the SA submodality type responded in the low flutter range (between 10 and 20 Hz), that S1 neurons of the QA type responded in the flutter range (10–40 Hz), and that S1 neurons of the Pacini (PC) type responded in the vibration range (above 40 Hz) (11). Differences between previous results (11) and ours could be due to the stimulus protocols. Furthermore, in the previous study used to classify the dynamic responses as a function of the stimulus frequency for SA, QA, and PC neurons, the stimulus amplitude used was at the threshold level (11), whereas in our study we used

frequency, a fixed frequency (22 Hz) and duration (500 ms) were used during categorization of amplitude, and both frequency (44 Hz) and amplitude (50 μm) were maintained fixed during categorization of the stimulus duration. Thus, categorization is made as a function of one sensory feature only. While the monkey

Fig. 1. Stimulus sets and categorization behavior (A, C, and E). Trials began when the stimulator probe tip indented the skin of one fingertip of the monkey’s restrained right hand (probe down, PD); the monkey reacted by placing its left, free hand on an immovable key (key down, KD). After a variable prestimulus period (1–3 s), a vibratory stimulus of variable frequency (A), amplitude (C), or duration (E) was presented on the skin of one digit. Following the stimulus presentation period, the monkey waited for 2 s until the probe was retracted (PU, probe up); the animal removed its free hand from the key (KU, key up) and pressed one of two PBs to report whether the stimulus was high or low in the case of frequency and amplitude sets and short or long in the case of duration sets. Lateral and medial buttons were used for reporting the stimulus as high or low and as short and long, respectively. Stimuli in a set were randomly interleaved in a run. (B) Behavioral responses in the frequency categorization tasks. Green PT curve (mean ± SD) shows categorization for the stimulus set with frequencies ranging between 10 and 30 Hz. Red curve (mean ± SD) shows categorization for the stimulus set with frequencies ranging between 14 and 78 Hz. (D) Behavioral responses in the amplitude categorization task. Green PT curve (mean ± SD) shows categorization for the stimulus set with amplitudes ranging between 20 and 80 μm. Red curve (mean ± SD) shows categorization for the stimulus set with amplitudes ranging between 42 and 138 μm. (F) Behavioral responses in the duration categorization task. Green PT curve (mean ± SD) shows categorization for the stimulus set with durations ranging between 0.050 and 0.550 s. Red curve (mean ± SD) shows categorization for the stimulus set with durations ranging between 0.330 and 1.170 s. PT, psychometric threshold; X0, the value (mean ± SD) that corresponds to frequency, amplitude, or duration where the probability called higher was equal to 0.5 in the logistic fit.

Fig. 2. Responses of a S1 neuron during the categorization of stimulus frequencies. (A and B)Raster plots. (C and D) Here, the neuron responded as a function of the stimulus frequency. Black dots represent firing rates for each single trial (usually 10 stimulus repetitions). S, value of the slope.
stimulus amplitudes above the threshold. Clearly, this shows that depending on the stimulus protocol, S1 neurons of the SA and QA types respond to both flutter and vibration frequencies. During recording sessions, we did not record PC neurons, and therefore, we could not test their dynamic responses in the frequency categorization task.

It is well known that S1 neurons (areas 3b and 1) increase their firing rates as a function of the increasing stimulus amplitude and that these responses account for the monkey's detection performance (1). All these studies were made using a fixed stimulus frequency (20 Hz), and the amplitude threshold was usually between 7 and 12 μm. In our amplitude categorization task, we used a wide range of stimulus amplitudes while maintaining fixed the frequency (22 Hz) and duration (500 ms). We recorded 101 S1 neurons during the amplitude categorization task, with the set ranging between 20 and 80 μm, and 94 S1 neurons tested with the set ranging between 42 and 138 μm. We found that both SA neurons (n = 29, 28.7% of the 101; n = 38, 40.43% of the 94) and QA neurons (n = 72, 71.3% of the 101; n = 56, 59.6% of the 94) responded similarly. Fig. 3 A and B shows an example neuron showing a wide range of responses to the stimulus amplitude. Thus, both SA and QA neurons showed the same type of dynamic responses to the stimulus amplitude sets. Although not surprising, S1 neurons showed a wide range of responses during the amplitude categorization task, but see below.

A previous study showed that the psychophysical discrimination performance is affected by the stimulus duration (9), but this variable has not been tested further during recordings of S1 neurons. Monkeys were trained to categorize stimulus duration, using the two stimulus sets illustrated in Fig. 1E and the psychophysical performance shown in Fig. 1F. As indicated previously, we maintained the stimulus frequency fixed at 44 Hz and the stimulus amplitude fixed at 50 μm. In the first stimulus duration set, we delivered two extreme vibrotactile stimulus durations, 50 ms and 550 ms, and asked the animal to report which was of short or of long duration by pressing one of two PBs with the free hand. Monkeys learned this rule in a few trials, and we then ran the stimulus set with durations between 50 and 550 ms. Monkeys switched in a few trials for another stimulus duration set, from 330 to 1,170 ms. Fig. 4A and B shows a typical response for an example S1 neuron. Fig. 4 C and D shows the dynamics of the responses with these two stimulus sets. As for the S1 neurons tested with the frequency and amplitude categorization tasks, all neurons encoded the stimulus duration in both stimulus duration sets. We recorded 82 S1 neurons during the stimulus duration set ranging from 50 to 550 ms and 61 S1 neurons with the stimulus duration set ranging from 330 to 1,170 ms. We found that both SA neurons (n = 22, 26.8% of the 82; n = 15, 24.6% of the 61) and QA neurons (n = 60, 73.2% of the 82; n = 46, 75.4% of the 61) responded similarly. Thus, both submodality types of S1 neurons have the capacity to respond to a wide range of stimulus durations and might have profound implications for perceiving the duration of a stimulus delivered to the skin.

One last question associated with the specificity of the responses of S1 neurons during the categorization tasks: Do they encode all of the sensory features of the vibrotactile stimulus or only one? To further address this question, we recorded 63 S1 neurons that were tested with each stimulus categorization set: frequency, amplitude, or duration. We found that almost a third of the S1 neurons (n = 17, 26.98%) encoded the three sensory features of the vibrotactile stimulus. Another third of the S1 neurons encoded more than one sensory feature. For example, 12 neurons (19.04%) encoded both stimulus frequency and amplitude, six neurons (9.52%) encoded both stimulus frequency and duration, and five neurons (7.93%) encoded both stimulus amplitude and duration. An interesting group of S1 neurons responded exclusively to the stimulus frequency (n = 8, 12.69%), amplitude (n = 7, 11.11%), or duration (n = 8, 12.69%). These results suggest that a third of the S1 neurons recorded encode exclusively one single stimulus feature of the vibrotactile stimulus and that two thirds have the capacity to encode more than one single sensory feature of the vibrotactile stimulus.

S1 Responses Relative to the Categorical Performance of Vibrotactile Stimulus Features. Having quantified the responses of S1 neurons as a function of each stimulus feature, we proceeded to determine whether each of these neural signals carried physiological information that might be associated with the animal's psychophysical behavior. For each neuron, we computed neuro- metric (NT) functions by using the firing rate values associated with the stimulus frequency, amplitude, or duration (Materials and Methods). We show in Fig. 5 A–L the relationship between the psychometric (PT) and NT functions for the three example neurons shown in Figs. 2–4 during the categorization of frequency, amplitude, or duration. Fig. 5A shows that the animal's PT threshold during the frequency categorization task (PT = 1.35 Hz) is almost similar to the NT function (1.51 Hz), with a strong relationship between the two values, calculated as threshold ratio (TR = 0.89). Indeed, the mean TR (1.12) calculated in the neural population with the stimulus set of frequency in the range of 10–30 Hz resulted in close correspondence between behavior and neuron (Fig. 5G). A close correspondence was also observed between the PT (3.39 Hz) and NT (2.57 Hz) TR (1.31) in the same neuron using the stimulus set with the range between 14 and 78 Hz (Fig. 5B). A close mean TR value was obtained at the population level (TR = 0.8; Fig. 5F). A similar correspondence between behavior and neuron was also found at the single and population levels for the neurons that responded to the stimulus amplitude and duration. For example, Fig. 5C shows both PT (4.65 μm) and NT (4.42 μm) thresholds for the example neuron shown in Fig. 3A during the categorization of amplitudes between 20 and 80 μm. Clearly, the TR shows a 1–1 relationship (TR = 1.05). Similar values were found with the extended stimulus amplitude set between 42 and 138 μm (PT = 8.32 μm, NT = 7.38 μm, and TR = 1.12; Fig. 5D). Fig. 5I and J shows the mean TRs with the two stimulus amplitude sets suggesting close correspondence between behavior and neuronal population.
The neurophysiological results suggest an encoding scheme in S1: from neurons that encode all sensory features of the vibrotactile stimulus to neurons that specifically encode only one feature. Third, the responses of S1 neurons correlate with the animal’s categorization behavior but do not predict the animal’s choice. We hypothesize that the dynamic representation of each sensory feature in S1 might serve for further downstream processing that leads to the monkey’s psychophysical behavior observed in these categorization tasks.

Monkeys categorized the vibrotactile stimulus on the basis of one single sensory feature. This was forged during the training period, as they learned to identify stimulus categories as high versus low (for frequency and amplitude categorization sets) and stimulus categories as short versus long (duration categorization sets) of the vibrotactile stimuli. To perform categorization of each sensory feature, it is very likely that the monkeys’ somatosensory network produced a “mnemonic template” of the edges of the stimulus features during the training periods (low and high values, and short and long values). This mnemonic template must read and classify the sensory feature to generate a categorization process. Although this process has been investigated using visual, complex stimuli (13–16), none of the investigations have investigated how the different components of the visual stimulus are represented in early visual cortex. In this respect, one important constraint imposed for any sensory modality is how an early sensory representation gives rise to the categorization process. In fact, the problem of categorization was addressed before in a somatosensory speed categorization task (17), but it was unclear whether in this task monkeys categorized the speed or the duration of the moving tactile stimulus (18). From the responses recorded in parietal and frontal lobe areas, it appears that the categorization process is computed downstream of the sensory cortex (13–16, 19, 20). However, which is the precise contribution of the sensory cortex in perceptual categorization?

We focused on the encoding capacities of both SA and QA neurons of the S1 cortex while the monkeys categorized sensory features of the vibrotactile stimulus. The results show that both submodality types of S1 neurons have the capacity to encode each stimulus feature of the vibrotactile stimulus. For those neurons that could be tested during the frequency, amplitude, or duration categorization tests (n = 63), the following encoding scheme was obtained: Almost a third encoded the three stimulus features (n = 17, 26.98%), another third encoded two sensory features (frequency and amplitude, n = 12, 19.04%; frequency and duration, n = 6, 9.52%; and amplitude and duration, n = 5, 7.93%), and a third encoded only one stimulus feature, equally distributed (frequency, n = 8, 12.69%; amplitude, n = 7, 11.11%; and duration, n = 8, 12.69%). Although the number of neurons studied with the three stimulus categorization sets might not be sufficient, we could speculate that in S1 there is a hierarchical encoding scheme. However, it is difficult to document this fact with the current findings. For example, are neurons that encode one sensory feature of the vibrotactile stimulus at the end of the hierarchical encoding scheme, or do those encode all of the sensory features? Also, whether this is constructed in the S1 circuit or imposed by the somatosensory thalamus remains to be determined by the simultaneous recordings of neurons of these two structures during the categorization tasks. Whatever the answers to these questions are, the results show that in S1 there is a repertoire of neural responses that account for the animal’s
psychophysical categorization for each sensory feature of the vibrotactile stimulus.

Our results show that there is a close correspondence between the NT and PT categorization behavior. Indeed, previous studies have studied the sensitivity of S1 neurons to different stimulus parameters, but few have shown whether this accounts for the psychophysical behavior (2). In our task, monkeys categorized different stimulus set configurations, and S1 neurons reflected this fact. However, S1 neurons did not predict the animal’s choice. This is consistent with previous findings in amplitude and frequency vibrotactile discrimination tasks (1, 2). In fact, these studies have shown that downstream areas to S1 encode mostly the cognitive components of these tasks, including the animal’s choice (21, 22). This suggests that there is a transformation of the vibrotactile stimulus from S1 to downstream areas. However, the presence of S1 neurons that encode multiple features or only one feature suggests some degree of specialization that could impact downstream networks. In other words, what is represented downstream of S1? It is possible that depending on the task demands, the neuronal circuits downstream of S1 could encode all stimulus features, but this capacity could be also subserved by intermingled but sensory feature-specific neurons. Therefore, studies are needed to show the encoding scheme(s) downstream of S1 during feature categorization of the vibrotactile stimulus.

Materials and Methods

Categorization Task. This study was performed on two male monkeys, *Macaca mulatta,* 5–7 kg. Monkeys were trained to categorize whether the sensory feature of a vibrotactile stimulus was high or low (frequency or amplitude) and of short or long duration. The monkey sat on a primate chair with its head fixed. The right hand was restricted through a half cast and kept in a head fixed. The right hand was restricted through a half cast and kept in a right, restrained hand, via a computer-controlled stimulator (2-mm round tip; BME Systems). The initial indentation was 500 μm (PD; Fig. 1 A, C, and E). Vibrotactile stimuli were trains of short mechanical pulses. Each of these pulses consisted of a single-cycle sinusoid lasting 20 ms (2). In separate blocks of trials, monkeys categorized only one feature of the mechanical vibration delivered to the glabrous skin of one fingertip: frequency (Fig. 1A), amplitude (Fig. 1C), or duration (Fig. 1E). For example, in the case of frequency, monkeys first categorized two extreme stimulus frequencies, 10 and 30 Hz, and reported which was low or high by pressing one of two Pbs with the left, free hand. They performed this test in a few trials. We then presented a block of trials with frequencies ranging between 10 and 30 Hz (Fig. 18, green plot). Monkeys then switched to categorization of frequencies ranging between 14 and 78 Hz (Fig. 1B, red plot), provided they first performed a few trials with the two new extreme frequencies, 14 and 78 Hz. This protocol was followed when the monkeys had to categorize the stimulus amplitude (Fig. 1 C and D) or stimulus duration (Fig. 1 E and F). It is important to emphasize that the stimulus amplitude (50 μm) and duration (500 ms) were maintained fixed during categorization of frequency, at a fixed frequency (22 Hz) and duration (500 ms) during categorization of amplitude (20–80 μm), and both frequency (44 Hz) and amplitude (50 μm) maintained fixed during categorization of the stimulus duration. Thus, categorization was made as a function of one stimulus feature only. The animal was rewarded for correct categorizations with a drop of liquid. Performance was quantified through PT techniques (Fig. 1 B, D, and F) (1, 2). Monkeys were handled according to the institutional standards of the National Institutes of Health and Society for Neuroscience. All protocols were approved by the Institutional Animal Care and Use Committee of the Instituto de Fisiología Celular, Universidad Nacional Autónoma de México.

Recordings. Neuronal recordings were obtained with an array of seven independent microelectrodes [2–3 MΩ (23)] inserted into S1 (areas 3b and 1), contralateral (left hemisphere) to the stimulated hand. We collected data using the stimulus sets illustrated in Fig. 1, usually 10 trials per stimulus. We used well-established electrophysiological and anatomical criteria to distinguish between cortical areas (1, 2). We recorded S1 neurons with cutaneous receptive fields confined to the distal segments of the glabrous skin of digits 2, 3, or 4 and had SA or QA properties (1, 2). For each studied neuron, the stimulus was delivered to the center of its cutaneous receptive field.

Data Analysis. We analyzed the responses of S1 neurons while the monkey performed the categorization tasks. All neurons had small cutaneous receptive fields located in the distal segment of one digit (fingertips 2, 3, 4, or 5). Stimuli were delivered to the center of the neuron’s receptive field. We considered a task-related response, if the distribution of the firing rates during the stimulation period was statistically different from a period immediately before trial initiation (ROC test, α = 0.01) (2, 24). The relationship between the stimulus and the neuron’s firing rate elicited during the
stimulation period (500 ms) was quantified using linear regression analysis (firing rate = slope \times stimulus categorization + basal firing rate). For the analysis, only slopes statistically different from zero were considered (permutation test, n = 1,000; P < 0.05) (24).

NT curves based on firing rates were constructed according to the model described previously (1). On each trial, we obtained the maximum firing rate in a 500- or 50-ms window that was displaced every 1 ms in the 1.5-s period between the stimulus onset and the probe being lifted up (PU). NT curves were constructed as the proportion of trials in which the maximum firing rate reached or surpassed a criterion level (1). For each neuron, this criterion was chosen to maximize the number of hits. PT and NT fits were obtained by fitting a Boltzmann equation. Lower and upper Boltzmann was chosen to maximize the number of hits. PT and NT fits were obtained according to the same criteria. For each curve, categorization threshold was calculated when the stimulus categorization of the monkey/neuron performance reached 50% categorization. The categorization modulation of the curve was the difference in categorization probability between the maximum and minimum values of the stimuli. This quantity accounted for how much the monkey/neuron performance varied within the relevant interval. The slopes for individual and population curves were calculated within the interval where the probability of categorization ranged between 0.4 and 0.6. The slopes and shapes of the curves indicated the sensitivity of the monkey/neuron to the stimulus. PT slopes were compared with their NT counterparts using a Wilcoxon rank test (\alpha = 0.05) (25).

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