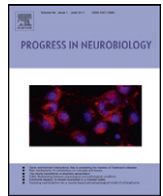




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## Conversion of sensory signals into perceptual decisions

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### ABSTRACT

A fundamental problem in neurobiology is to understand how brain circuits represent sensory information and how such representations give rise to perception, memory and decision-making. We demonstrate that a sensory stimulus engages multiple areas of the cerebral cortex, including primary sensory, prefrontal, premotor and motor cortices. As information transverses the cortical circuits it shows progressively more relation to perception, memory and decision reports. In particular, we show how somatosensory areas on the parietal lobe generate a parameterized representation of a tactile stimulus. This representation is maintained in working memory by prefrontal and premotor areas of the frontal lobe. The presentation of a second stimulus, that monkeys are trained to compare with the first, generates decision-related activity reflecting which stimulus had the higher frequency. Importantly, decision-related activity is observed across several cortical circuits including prefrontal, premotor and parietal cortices. Sensory information is encoded by neuronal populations with opposite tuning, and suggests that a simple subtraction operation could be the underlying mechanism by which past and present sensory information is compared to generate perceptual decisions.

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**Abbreviations:** S1, primary somatosensory cortex; S2, second somatosensory cortex; VPC, ventral promotor cortex; DPC, dorsal promotor cortex; MPC, medial promotor cortex; PFC, prefrontal cortex; M1, primary motor cortex.

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## 1. Introduction

More than two thousands years ago, based on an intellectual *tour de force*, the Greek philosopher Democritus (430–420 B.C.) suggested that objects of the external world were constituted of moving atoms that reached the brain, where they generated dynamic images that are processed for thinking (Jung, 1984). For him, this process provided the raw material for sensation, perception, learning and action. In this manner, the subject could voluntarily use these internal representations to guide thoughts and actions. Unintentionally, Democritus suggested a working hypothesis that many contemporary scientists use to investigate where and how in the brain a sensory representation transforms in perception, memory and action. But, in now days, what is known about this millenary hypothesis?

It was Adrian (1928) the first to scientifically test this ancient hypothesis. He recorded the peripheral fibers innervating skin receptors and observed how the firing rates varied as a function of the stimulus strength applied to the skin. These experiments opened a vast field of research aimed to elucidate how sensory inputs are represented in the peripheral nervous systems (Hartline et al., 1956; Johnson and Hsiao, 1992; Werner and Mountcastle, 1965; Connor et al., 1990). This experimental approach paved the way for new questions associated with the problem of neural coding. The underlying belief was that unraveling the neural representations of sensory stimuli, from periphery to early stages of cortical processing, was key to understanding brain function. Indeed, investigations across the sensory systems have shown how neural activity represents the physical or chemical parameters of sensory stimuli in both the periphery (Connor et al., 1990; Axel, 2005; Barlow, 1957; Buck, 2005; Hartline et al., 1956) and central brain areas (Creutzfeldt and Nothdurft, 1978; Hubel and Wiesel, 1998; Merzenich and Brugge, 1973; Mountcastle et al., 1969; Ruiz et al., 1995; Stettler and Axel, 2009). These results constitute the bases for new questions relating to the cognitive processing of sensory inputs. For example: where and how in the brain are the sensory representations converted into perceptual decisions? Specifically, what components of the neuronal responses evoked by a sensory stimulus are directly related with perception and decision making? Where and how in the brain the sensory information is stored in memory? How stored sensory information combines with current sensory information and how the resulting interactions are linked to perceptual reports?

Here we review the available experimental evidence that relates to the above questions using somatosensory detection and discrimination tasks in which the neuronal activity across cortex can be directly linked to the monkeys' psychophysical detection and discrimination reports. This comparative analysis allows tracking neuronal activities from distinct cortical circuits that might be associated with the diverse components of these two tasks.

## 2. Sensory detection

Detecting sensory stimuli is among the simplest perceptual experiences and is a prerequisite for any further sensory experience. A fundamental problem posed by sensory detection tasks is that repeated presentations of a near-threshold stimulus unpredictably fail or succeed to generate a sensory percept. Where in the brain are the neuronal correlates of these varying perceptual judgments? Pioneer studies on the neuronal correlates of sensory detection showed that, in the case of vibrotactile stimuli, the responses of primary somatosensory cortex (S1) neurons account for the measured psychophysical accuracy (Mountcastle et al., 1969). However, direct comparisons between S1 responses and detection performance could not be addressed and, therefore, it is not clear whether the activity of S1 accounts for the variability of the behavioral responses. In these earlier studies, psychophysical performance was measured in human observers and S1 recordings were made in anesthetized monkeys.

### 2.1. Psychophysics of sensory detection

The detection of sensory stimuli has been recently addressed by de Lafuente and Romo (2005, 2006). These authors trained monkeys to perform a vibrotactile detection task. On each trial, the animal had to report whether the tip of a mechanical stimulator vibrated or not (Fig. 1A). The 20 Hz sinusoidal stimuli were delivered to the glabrous skin of one fingertip. Crucially, they varied in amplitude across trials. Stimulus-present trials (amplitude > 0  $\mu\text{m}$ ) were interleaved with an equal number of stimulus-absent trials in which no mechanical vibrations were delivered (amplitude = 0  $\mu\text{m}$ ). Depending of the monkeys' behavioral reports, trials could be classified into four types: hits and misses in the stimulus-present condition, and correct rejections and false alarms in the stimulus-absent condition (Fig. 1B). Stimulus detection thresholds were calculated from the behavioral responses (Fig. 1C). By simultaneously recording the behavioral responses along with the neuronal activity in the brain, these studies attempted to elucidate the neuronal mechanisms underlying the detection of sensory stimuli.

### 2.2. Neuronal S1 activity during sensory detection

de Lafuente and Romo (2005) simultaneously characterized the activity of S1 neurons (areas 3b and 1) and the monkey's psychophysical performance. Figs. 1C and 2A show the monkey's psychometric curve and the spike trains of an S1 neuron recorded in the same trials. To test whether the responses of S1 neurons accounted for the monkey's psychophysical performance, de Lafuente and Romo (2005) calculated neurometric detection curves and compared them with the psychometric curves. The proportion of 'yes' responses for neurometric curves was defined as

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