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# Coding processes involved in the cortical representation of complex tactile stimuli

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## Abstract

To understand how information is coded in the primary somatosensory cortex (S1) we need to decipher the relationship between neural activity and tactile stimuli. Such a relationship can be formally measured by mutual information. The present study was designed to determine how S1 neuronal populations code for the multidimensional kinetic features (i.e. random, time-varying patterns of force) of complex tactile stimuli, applied at different locations of the rat forepaw. More precisely, the stimulus localization and feature extraction were analyzed as two independent processes, using both rate coding and temporal coding strategies. To model the process of stimulus kinetic feature extraction, multidimensional stimuli were projected onto lower dimensional subspace and then clustered according to their similarity. Different combinations of stimuli clustering were applied to differentiate each stimulus identification process. Information analyses show that both processes are synergistic, this synergy is enhanced within the temporal coding framework. The stimulus localization process is faster than the stimulus feature extraction process. The latter provides more information quantity with rate coding strategy, whereas the localization process maximizes the mutual information within the temporal coding framework. Therefore, combining mutual information analysis with robust clustering of complex stimuli provides a framework to study neural coding mechanisms related to complex stimuli discrimination.

*Keywords:* Information theory; Neural coding; Stimulus feature extraction; Primary somatosensory cortex

## 1. Introduction

A major challenge in Neuroscience is to decipher how neural activity represents the physical features of objects with which animals interact. For instance, each degree of roughness scanned by whiskers corresponds both to a unique kinetic signature defined by a temporal profile of whisker velocity and to a distinct firing pattern, based on spike counts (Arabzadeh et al., 2005, 2006). Although most of the studies to date have used rate coding, several authors have emphasized the key role of spike timing in neural population coding (Borst and Theunissen, 1999). Using precise spike timing, the first spikes have been shown to transmit larger quantities of information about stimuli than the same spikes in rate coding, either in the barrel cortex (Panzeri et al., 2001) or in the cortical forepaw representation (Foffani et al., 2004).

Instead of whiskers, rats can use their forepaws to perceive object features, such as location, size, shape and texture (Bourgeon et al., 2004; Iwaniuk and Whishaw, 2000). We know that the forepaw representation in the S1 cortex is topographically organized (Coq and Xerri, 1998). This topographic organization provides a spatial frame of reference for location detection of stimuli applied on different forepaw locations. However, the large range of spatiotemporal responses in the S1 forepaw cortex (Tutunculer et al., 2006), such as found in the barrel cortex, may allow the extraction of the multidimensional kinetic features of objects or complex tactile stimuli.

Neural coding refers to how the central nervous system represents sensory information as patterns of action potentials emitted by neuronal populations. The neural coding problem is often formulated in terms of quantitizing a joint

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space $(R;S)$ (Mumey et al., 2004; Slonim et al., 2006; Nadal, 2002) where $S$ represents the input sensory stimuli and $R$ the set of possible neural activity patterns. Both of these spaces are high-dimensional and complex. We consider the sensory system robust and adaptive, in that it must represent similar stimuli in similar ways. Thus, individual input stimuli are not important for understanding neural function, but rather classes of input stimuli and their correspondence are the key to decipher the neural representation of complex stimuli. Following this idea, this study refers to a model in which neurons are selective for a small number of stimulus dimensions out of a high-dimensional stimulus space, and within this subspace similar sensory signals are clustered. The idea that Shannon's Information Theory (Shannon, 1948) is relevant for studying neural coding goes back to Attaneve (1954) and has received considerable attention these last few years (Bialek et al., 1991; Atick, 1992; Borst and Theunissen, 1999). In this paper first of all, we report generality on information theory in the neural coding context. Secondly, we present another information quantity: the "multi-information", useful to study neural representations of complex stimuli.

In this paper the simultaneous activity of S1 neuronal populations was recorded to explore the neural coding of location detection and kinetic feature extraction of complex stimuli, based on either spike count or spike timing. Location detection is related to the different sites of forepaw stimulation, while feature extraction refers to a compression process of the high-dimensional kinetic values (i.e. random, time-varying patterns of force) of complex tactile stimuli, as encountered in the natural environment. Are stimulus localization and feature extraction independent processes? What is the time course of these processes after stimulus onset, depending on rate or temporal coding? We used mutual information (MI) to measure the stimulus-response relationship, and different stimuli clustering strategies to separate each neural process. To our knowledge, this study is the first attempt to compare these two neural processes of stimulus identification and to use "multi-information" in the neural context.

## 2. Methods

### 2.1. Information theoretic framework

#### 2.1.1. Information carried by neuronal population response

Mutual information is a rigorous criterion to quantify how much information the neural responses convey about a sensory stimuli set (Bialek et al., 1991). We consider a time window $T$, associated with a sensory stimulus $s$ chosen with a probability $p(s)$ from a stimulus set $S = \{\mathbf{s_1},\mathbf{s_2},\ldots,\mathbf{s_m}\}$, during which the activity of $C$ neurons is recorded. The neuronal population response is denoted by the random variable $R = \{\mathbf{r_1},\mathbf{r_2},\ldots,\mathbf{r}_n\}$, where each component of the vector $\mathbf{r}_n = [r_n^1, r_n^2, \ldots, r_n^C]$ is the response of one neuron of the population within the time window $T$. Each neuronal response can be differently described depending on the coding framework. In a spike count code, the response is the number of spikes within the time window $T$. In a spike timing code, the response is a sequence of spike firing times. The MI between $R$ and $S$ is defined as the difference between the Shannon response entropy and the noise entropy (Shannon, 1948).

$$I(R;S) = H(R) - H(R|S) \tag{1}$$

where the entropy is

$$H(R) = -\sum_{\mathbf{r}\in R} p(\mathbf{r}) \log p(\mathbf{r})$$

and the noise entropy

$$H(R|S) = -\sum_{s\in S} p(s) \sum_{\mathbf{r}\in R} p(\mathbf{r}|s) \log p(\mathbf{r}|s)$$

The mutual information can be written as

$$I(R;S) = \sum_{s\in S} p(s) \sum_{\mathbf{r}\in R} p(\mathbf{r}|s) \log \frac{p(\mathbf{r}|s)}{p(\mathbf{r})} \tag{2}$$

$p(\mathbf{r}|s)$ is the probability of simultaneously observing a particular response $\mathbf{r}$ conditional to the stimulus $s$, and $p(\mathbf{r}) = \sum_{s\in S} p(s)p(\mathbf{r}|s)$ is its average across all stimuli.

#### 2.1.2. Mutual information for three random variables

In this section we address inequalities involved in Shannon's information measures, for three discrete random variables. A region in $\mathbb{R}^{2n-1}$, denoted by $\Gamma^*$, is identified to be the origin of all information inequalities involving $n$ random variables in the sense that all such inequalities are partial characterizations of $\Gamma^*$. Further theoretical precisions can be found elsewhere (Yeung, 1997).

In this study we address the issue of dependence between two processes: stimulus feature extraction and stimulus localization. Within this framework, we introduce two other variables $K$,$L$ describing the stimulus set $S$ (i.e. $K = f(S)$ and $L = g(S)$). $K$ is the random variable which describes the stimulus kinetic features extraction $K = \{k_1,k_2,\ldots,k_K\}$ and $L$ is the random variable which describes the different stimuli locations $L = \{l_1,l_2,\ldots,l_L\}$. Using the chain-rule of information (Cover and Thomas, 1991) we can develop the MI

$$\begin{aligned} I(R;K,L) &= I(R;K) + I(R;L|K),\\ I(R;K,L) &= I(R;L) + I(R;K|L) \end{aligned} \tag{3}$$

where $I(R;K,L)$ is the MI between the neural response $R$ and the intersection of both stimuli sets $K$ and $L$ (Fig. 1). This quantity can be rewritten using the mutual information definition equation (1)

$$I(R;K,L) = \sum_{k\in K} \sum_{l\in L} p(k,l) \sum_{\mathbf{r}\in R} p(\mathbf{r}|k,l) \log \frac{p(\mathbf{r}|k,l)}{p(\mathbf{r})} \tag{4}$$

where $p(\mathbf{r}) = \sum_{k\in K} p(k) \sum_{l\in L} p(l) p(\mathbf{r}|k,l)$

$I(R;K)$ is the MI between the neural response and the stimulus, considering only the kinetic features, so that the stimuli are clustered according to their time-varying intensity. $I(R;L)$ is the MI between the neural response and the stimulus, considering only its location. $I(R;L|K)$ is the MI between the neural response and the stimulus location knowing its kinetic features. $I(R;K|L)$ is the MI between the response and the stimulus kinetic features knowing its location.

The non-negativity property of the MI (Cover and Thomas, 1991), gives the following expressions

$$\begin{aligned} I(R;K,L) &\geqslant I(R;K),\\ I(R;K,L) &\geqslant I(R;L) \end{aligned} \tag{5}$$

From these inequalities we can write a lower bound of the MI between the neural response and both the stimulus kinetic feature extraction and stimulus localization

$$I(R;K,L) \geqslant \frac{1}{2}[I(R;K) + I(R;L)] \tag{6}$$

Suppose the random variables $R \to K \to L$ form a Markov chain, then the data-processing inequality (Cover and Thomas, 1991) gives

$$\begin{aligned} I(R;K|L) &\leqslant I(R;K)\\ I(R;L|K) &\leqslant I(R;L) \end{aligned} \tag{7}$$