

# Separate but equal: Different kinds of information require different neural representations

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## 1 Introduction

Information processing systems have to deal with a variety of different types of information. The most obvious distinction is that between input and output. In the simplest technical systems this may be all that is required and behavior can be completely characterized as a relation between input and output variables. In more complex artificial system and, we surmise, in *all* biological neural systems, several other types of information are relevant, the internal states of the system. We are not concerned here how those states are determined by the genetic heritage of the animal (or the hardware design of the machine) and its “experience” (i.e., input received at previous times). We also have only peripheral interest in the modification of the states in the course of the system’s behavior; instead, we will take the existence of those states as granted and study their interaction with each other and with the input/output variables. In particular, we are concerned with the representation of the different states and types of information and the interactions between these representations.

## 2 Neural representations

The vertebrate nervous system continuously solves a multitude of different tasks including perception, generation of motor behavior, control of metabolic variables etc. It has been known for a long time that different tasks are associated with different parts of

the brain, e.g. control of the visceral functions in the brainstem, visual perception in the more caudal portions of neocortex, emotion by the amygdala and related structures etc. Even within one perceptual modality, different features of a percept are handled preferentially by different parts of the brain (e.g. color and motion in cortical areas V4 and MT, respectively). This division of labor leads to specific theoretical problems, in particular the “binding problem” which has been discussed extensively over the last decades (for an excellent collection of reviews see the special issue in *Neuron* **24**, Sept. 1999) and to which we will briefly return later. What is perhaps less appreciated is that despite this spatial segregation of functions and the functional advantages this organization seems to have for the organism, at least some of these tasks have to be solved by the same neural populations. The reason is that the different variables have to interact with each other.

The central question we are asking here is how these different types of information share the same neural substrate? The traditional view is that the response characteristics of a neuron are fully characterized by its mean firing rate, as quantified, e.g., by “tuning curves” (plot of firing rate as function of stimulus properties) and “receptive fields” (part of sensory space in which stimuli generate changes in firing rate). We argue, however, that there is a functional need for more than one type of neural signal and that the temporal structure of spike trains provides the required additional degrees of freedom. The existence and possible importance of temporal

structures in spike trains has been emphasized repeatedly (for some classical work see Poggio & Viernstein, 1964; Werner & Mountcastle, 1965) Increasingly stronger indications that neuronal spike trains contain information going beyond that in the firing rate is provided by more recent information theoretical analyses which indicate that the amount of information transmitted far exceeds that due to the firing rate, and that the excess information is due to temporal coding<sup>1</sup> (Reinagel & Reid, 2000; Reich, Mechler, Purpura, & Victor, 2000).

### 3 Selective attention

In the remainder of this essay, we will focus on one internal state variable, namely selective attention. The main reason for this limitation is that more is known about the representation of selective attention than about any other non-sensory and non-motor functional state of the primate nervous system. We surmise, however, that the basic problem is similar for all state variables and, although the details of their representation may differ, a single biophysical variable (mean frequency of action potentials) is not suitable for the representation of simultaneously present and inherently different quantities.

Selective attention is the capability of organisms to select a part of the information provided by the peripheral nervous system for detailed processing and to suppress the remainder (for a functional definition of selective attention see Niebur & Koch, 1998). The influence of selective attention on the representation of sensory information has been studied as a modulatory effect of sensory processing. There are several reasons why attention is much better understood than other such modulatory effects (e.g. emotions), not the least being that the quantitative

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<sup>1</sup>We do not want to imply that temporal structures in spike trains are the only signals being used to transmit and process information about internal state variables. The influence of neuromodulators is well-known to exist though not well-understood. For instance, it seems highly likely that emotional influences are exerted at least partly by changing “set points” of operation in complex large-scale networks (LeDoux, 2000). These are difficult questions to study and it may well turn out that insight will be fastest in invertebrate networks which are not only much simpler but also much easier to study (Marder, 1994).

study of attention goes back for more than a century (Helmholtz, 1867; James, 1890). In addition, the study of attention has progressed along a large spectrum of levels of complexity, from the early psychological studies at the level of the organism (ibid) which is still very much pursued in psychophysical research (for a recent review see Egeth & Yantis, 1997) over methods using large networks of neurons in imaging methods (Burton, Abend, MacLeod, Sinclair, Snyder, & Raichle, 1999), to the single cell level (Mountcastle, Andersen, & Motter, 1981; Moran & Desimone, 1985; Treue & Maunsell, 1996; Hsiao, O’Shaughnessy, & Johnson, 1993; Steinmetz & Constantinidis, 1995)

With few exceptions, the underlying assumption on the modulatory influence of selective attention on neural responses is that attention modifies the neural firing rates which are reported as functions of the attentional state. It is indeed found that in many cases, firing rate does change with the attentional state of the animal.

We argue here that from a functional point of view, the firing rate is not well-suited to serve as a representation of attention. The reason is that the firing rate is being used to represent stimulus properties at the input side and motor commands at the output side. The reasons *why* this is the case may be lost in the mist of evolutionary history but it seems plausible that the primary information about the environment and the primary type of control commands are based on this very simple code which may have evolved directly from the activity level of electrotonic potentials (Niebur & Erdős, 1988). Furthermore, this code does not depend on any other variable (e.g. activity of other neurons which is the case for synchrony codes) which facilitates processing given that peripheral input and output is provided by cells which have little or no communication neither between them nor from the more central parts of the nervous system.

Rate codes are simple, easy to generate and relatively robust (Softky, 1995). It is possible that simple organisms which were limited to very simple input-output relations (like simple reflexes) could get by entirely with such a simple coding schemes and, indeed, it has been suggested (Niebur & Erdős, 1993) that there may be whole organisms that never use the standard action potentials exemplified by the

Hodgkin-Huxley dynamics. This suggestion has been supported by recent experimental data (Goodman, Hall, Avery, & Lockery, 1998)

Our main argument here is that a pure activity code is too limited for complex organisms. The reason is the above-mentioned argument that different *types* of information share the same physical substrate. The emotional state of the animal, the sensory input, the motor commands, the level of satiety and a myriad of other information is being coded by the same set of neurons, notwithstanding the level of spatial segregation already mentioned. Certainly, there are specialized sections of the brain which deal mainly with specific tasks: cortical area V1 with early vision, pyriform cortex with olfaction, the medulla with the control of breathing etc. However, spatial segregation is only possible to a certain extent and the different subsystems clearly have to interact. If one of several simultaneously present stimuli is to be selected then the neural representation of the attentional state (which of the stimuli is to be selected) has to interact with the neural representation of the stimuli.

What we propose here is that this requires that the same neural substrate uses different operating modes which are “nearly” independent of each other. Of course, the “nearly” is important: while we emphasize here their independence, complete independence is not desirable since that would mean that no interaction would occur. But the need for interaction is one of the prime reasons why these different signals have to share the same substrate<sup>2</sup> and completely orthogonal representation would preclude interaction. In our example of selective attention, attentional influences eventually have to lead to changes in firing rate since only the latter are signals which lead to motor responses and all behavior is eventually due to motor responses. Likewise, attention is influenced by stimulus properties. While top-down influences clearly play a role (Desimone & Duncan, 1995; Usher & Niebur, 1996), a significant part of attentional influence is due to stimulus properties. What we find, therefore, is a mix of rate codes and temporal codes, and it is for this reason that attentional influences

<sup>2</sup>Another possible reason is economy of cells – the number of neurons in the nervous system is large ( $10^{10}$ ) but by no means infinite.

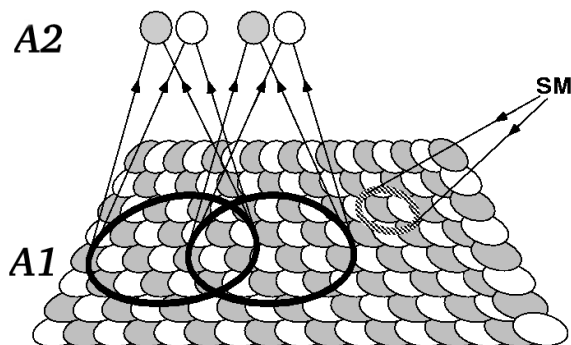


Figure 1: Attention modulates temporal structure in early cortex. The modulation is imposed from the “saliency map” SM (Koch and Ullman, 1985, Niebur and Koch 1996, Itti et al 1998) which influences the temporal structure of spike trains in an area in early cortex (A1). Neurons in this area respond differentially to sensory stimuli which is indicated by the shading of their overlapping receptive fields (gray and white). The attentional modulation functions as a “tag” which is decoded in higher cortical area A2. For details see Niebur et al (1993) and Niebur and Koch (1994).

were found in experimental paradigms in which only mean rates were determined.

Representing the attentional (or emotional etc) state purely in the firing rate would lead to a confounding of stimulus properties<sup>3</sup> (which we know are represented by the firing rate) with internal state properties. For instance, if the influence of selective attention consisted in increasing the firing rate of those neurons which respond to the attended stimulus, then a weak but attended stimulus would be indistinguishable from a strong but unattended stimulus.

## 4 Simultaneous representation of stimulus properties and attentional state

<sup>3</sup>We focus here on the input side, sensory input and neglect the output side for the sake of definiteness.

The solution to the problem is to have quasi-orthogonal representations. In particular, we have suggested (Niebur et al., 1993; Niebur & Koch, 1994) that the attentional state is represented in the temporal structure of spike trains at the time scale of milliseconds or tens of milliseconds while the stimulus properties are represented at the mean firing rate at longer time scales (hundreds to thousands of milliseconds). The computational models underlying these ideas (Niebur et al., 1993; Niebur & Koch, 1994, see also Figure 1) predict that the spike trains

1. should be suitable for representing state information, i.e. should have a non-trivial internal temporal structure
2. this structure should change with the attentional state

Recent data support both requirements. Steinmetz, Roy, Fitzgerald, Hsiao, Johnson, and Niebur (2000) found that responses of neurons in secondary somatosensory cortex (SII) of awake behaving monkey are synchronized and suggested that this synchrony could serve as an information-carrier (condition 1). In addition, and more importantly, they found that the synchrony status changed as a function of the attentional state, i.e. whether the stimulus to which the neurons responded is attended or not (condition 2). Similar results were obtained in the visual cortex of primates (R. Desimone, personal communication) and the somatosensory cortex of rodents (Roy & Alloway, 1999).

Note that these time scales correspond to those of the underlying phenomena: while attentional shifts occur every few tens of milliseconds<sup>4</sup> (Treisman & Gelade, 1980; Saarinen & Julesz, 1991), behaviorally relevant changes in stimulus properties rarely occur faster than 100ms which is about the highest rate at which separate perceptions can be formed (Biederman, 1972). If this correspondence of time scales holds for other internal states (and functionally it seems that it should) then the prediction is that internal states that change on slower scales, like emotions, should be represented by processes that change them-

<sup>4</sup>This is to be distinguished from much longer time scale related to attentional blink (Ward, Duncan, & Shapiro, 1996).

selves on slower scales, like neuromodulators acting on a time scale of seconds to minutes.

## 5 Concluding observations

Two more comments are in order. The first is that a coding scheme like that proposed here solves the so-called binding problem. This is the functional difficulty resulting from the spatially separate processing of different features of sensory stimuli and the resulting question of how the system keeps track of which feature “belongs” to which stimulus. In the proposed scheme, the problem is solved only for one of the stimuli, namely the attended one: all spike trains generated in response to this stimulus carry the temporal structure imposed by the attentional mechanism (see Fig. 1) and such structure will not be present for any other stimulus. It will therefore always be possible to distinguish between the attended stimulus and all others but not between those others. This makes clear predictions about limitations about perception, in particular the presence and properties of illusory conjunctions (erroneous association of features belonging to one stimulus to another simultaneously present stimulus). One prediction is that illusory conjunctions may occur between features of unattended stimuli: because neither of them has the attentional “tag” (see Fig. 1) attached to them they cannot be distinguished once the segregation of feature processing has occurred. Likewise, illusory conjunctions may occur between attended objects because the representations of *all* of them carry the tag. No illusory conjunctions should occur between attended and unattended stimuli. These predictions seem to be in agreement with observed data (Treisman & Schmidt, 1982). As a consequence, in order to be useful in situations where more than one stimulus is present (which are the only ones in which the binding problem even exists) a rapid change of the attended stimulus is required. This is in agreement with the fast movements of the focus of attention reported in psychophysics (Treisman & Gelade, 1980; Saarinen & Julesz, 1991).

The second observation is that in the proposed scheme, the long-raging discussion about temporal codes vs. rate codes comes to the salomonic resolu-

tion that both are correct. Except for sensors and motoneurons found at the extreme periphery, all neurons participate in the representation of different types of information, employing representations that vary at different timescales. For instance, neurons in sensory cortex in which strong attentional effects have been found use a mixed rate-temporal code to represent both stimulus features and attentional status. As a consequence, changes correlated with the attentional state are observed both in the firing rate (Moran & Desimone, 1985; Hsiao et al., 1993) and in the temporal structure (Steinmetz et al., 2000).

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