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Spatio-temporal dynamics of information processing in the Brain: Recent advances, current limitations and future challenges

Boris Burle^a, Clémence Roger^a, Franck Vidal^a, Thierry Hasbroucq^a

^aLaboratoire de Neurobiologie de la Cognition,
Aix-Marseille Université, CNRS, Marseille, France

Correspondence: B Burle, LNC-Pôle 3C, Université de Provence, Case C, 3 Place Victor Hugo, 13331 Marseille, cedex 3, France. E-mail: boris.burle@univ-provence.fr, phone +33 4 88 57 68 79, fax +33 4 88 57 68 79

Abstract. Understanding how the brain transforms sensory information into adapted motor behavior necessitates to track the flow of information in the brain space. One question of great importance is to what extent the various required cognitive operations overlap in time (can a response begin to be prepared before the end of stimulus evaluation?). Symmetrically, it is essential to understand what is the degree of localization of the elementary cognitive operations (Are the motor areas purely motor, or do they intervene also in sensory processing?). After a brief statement of the current theoretical questions, we will present some recent data regarding these issues. The general logic followed is to track the information flow backward, starting from the response up to the stimulus. We will then present some technical limitations hampering more precise investigations and conclude on the challenges for the next few years for real advancement on those topics

Keywords: Information processing, motor processing, EEG, Spatio-temporal dynamics

1. Introduction

We continuously receive sensory information from the environment. For our behaviors to be adapted to this environment, this sensory information has to be transformed into a motor code, through which our interactions with the environment are expressed. The question as to how the sensory codes are transformed into motor ones is one of the current challenges in cognitive neuroscience. One way to address this general question is to study the spatio-temporal dynamics of information processing in the brain, that is how the processing operations are organized in time and in space (of the brain areas). Both temporal and spatial dynamics can be considered along a continuum depending on the amount of overlap (both temporal and spatial) of the processing operations. We shall first present these two continuums. We will then present some how one can address those issues based on recent data and then raise some technical problems impeding further progress on these issues.

1.1. Temporal overlap

A minimal decomposition of information processing requires three types of operations: sensory processes, stimulus-response association and motor processes. The temporal dynamic of such processes can be described on a continuum from purely serial processes to parallel ones. In the serial extreme, process $n+1$ (for example stimulus-response association) cannot begin until process n has finished. Symmetrically, completely continuous models assert that as soon as process n receives any piece of evidence, it transmits continuously this information to process $n+1$ (see [Sternberg, 2001] for an overview). Along this continuum, a large palette of architectures is conceivable. It can even be conceived that the flow of information is not purely feed-forward, but that feedback from level $n+1$ on level n may occur. One important question is where, and under which conditions, cognitive processes lie on this continuum. For years, those questions have been addressed thanks to behavioral techniques. However, since the critical variable is the transmission of information between levels, only studying the product of the chain does not seem appropriate and investigating brain processes implementing those cognitive operations seems necessary.

Although EEG and MEG seem *a priori* the methods of choice, as we shall see later, there are currently technical limitations that impede such investigations.

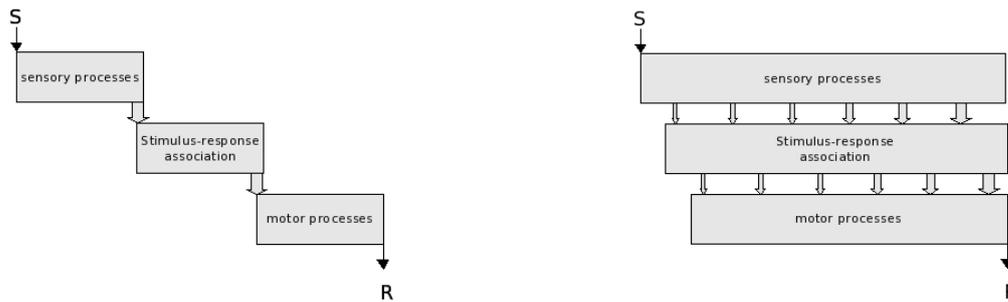


Figure 1. Schematic representation of the two extremes forms of information processing temporal organization: left, purely serial model; right, purely continuous model.

1.2. Spatial overlap

If one aims at understanding the dynamics of information processing, one needs to match neurophysiologic indices with cognitive operations. The way such a matching can be done largely depends on the conception one has of the so-called structure-to-function relationship. The history of neuroscience has oscillated between two extremes points of view: localization versus distribution of functions. At that stage, one clarification is in order since a common mistake pollutes this debate: the discussion of localization vs. distribution should be conceived only at the level of elementary functions. As elementary as it could be debating on whether a behavior is localized or distributed has no sense. Even the simplest behavior, requiring several cognitive operations, is necessarily distributed. The relevant question is whether the *elementary operations that compose* such a behavior are or not distributed over the brain. For example, a question like “does reaching a pen lying on a table require distributed areas?” is incorrectly posed, since such a *behavior* requires seeing the pen, planning a movement and executing it. An example of a more relevant question would be whether, in such a motor context, the visual processing of the pen also involved non *a priori* visual areas, like the motor ones [Requin and Riehle, 1995].



Figure 2. Schematic representation of pure localization of functions (left) and largely distributed functions. The black dots (●) represent visual neurons, whereas the white ones (○) represent motor neurons.

1.3. Orthogonality of these two continuums

For years, these two continuums have been confounded more or less implicitly on only one dimension, ranging from serial/localized to continuous/distributed. For example, “early” activation of the motor cortices has often been interpreted as reflecting continuous processes. However, the temporal and spatial dimensions *can* and *must* be dissociated. Indeed, operations may overlap in time (motor response could be prepared before stimulus evaluation is over) while these two operations remain perfectly separated in space (sensory processing limited to sensory areas, and motor processes to motor areas). Symmetrically, motor processes might well start after sensory processes have finished (no temporal overlap), but sensory and motor processes could partially be implemented in the *same* areas (spatial overlap).

Therefore, if one wants to use neurophysiological indices to track the temporal dynamic of information processing operations, it is necessary to also address their degree of spatial overlap.

2. Backwards analysis of the information processing flow.

For several years now, we have been studying the information processing flow in a backward fashion: starting from the response (*i.e.* the output of the system) to the stimulus. Such an approach has been motivated by the fact that studying the late stages of information processing makes it more likely to see the impact of previous stages on the current processing. In several studies, we first used electromyographic (EMG) activity that allowed us to evidence which experimental factors affect peripheral motor processes and which do not. We then went one-step further by analyzing information processing in the primary motor cortices (MI). In a between-response choice context, and by means of stimulation techniques (Hoffman reflex at the spinal level and transcranial magnetic stimulation – TMS), we have shown that just before the EMG onset the contralateral MI (involved in the incorrect response) is being *inhibited* [Burle et al., 2002; Hasbroucq et al., 2000] while the primary motor (MI) involved in the correct response is being activated. Such a activation/inhibition pattern is also observable with EEG [Tandonnet et al., 2006; Vidal et al., 2003], provided that appropriate deblurring methods (*e.g.* Surface Laplacian estimation) are used. Interestingly, the activities of the MIs are sensitive to some experimental manipulations (*e.g.* preparation [Tandonnet et al., 2006]), but others, more central, manipulations leave them unaffected. This differential sensitivity allows to investigate how and when information flow propagates to motor processes.

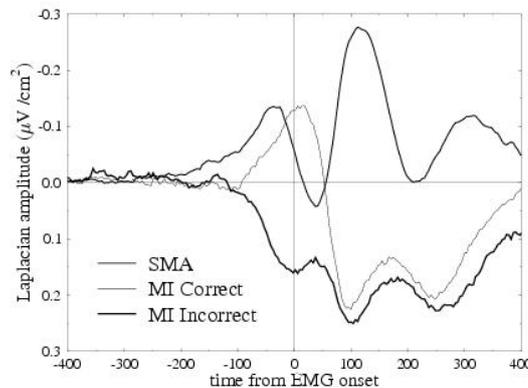


Figure 3. Time course of the activity recorded over the MI, and likely the SMA, around the response in a choice reaction time task. While the “correct” MI (*i.e.* contralateral to the correct response) is getting more active, the ipsilateral MI is inhibited. A fronto-central wave, likely originating from the SMA occurs about 50 ms before the MI. Adapted after [Vidal et al. 2003]

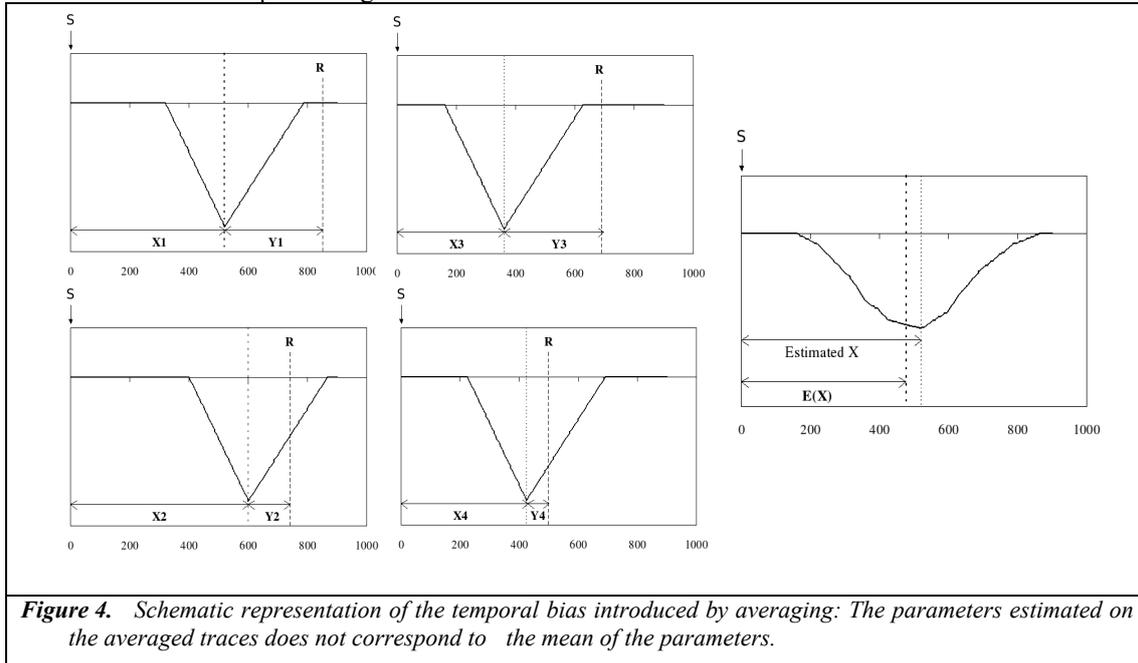
Laplacian estimation also revealed that premotor areas (like the Supplementary Motor Area – SMA) are activated slightly before the MI [Vidal et al., 2003]. Figure 3 shows an example of both the two MIs (electrodes C3 and C4) and the SMA (electrode FCz). In this particular case, the peak observed over the SMA occurred about 50 ms before MIs. This activity disappears when the subjects know in advance which response they will have to perform. Interestingly, the positivity observed ipsilateral to the correct response is also greatly reduced [Carbonnell et al., 2004], or even disappears, in this situation. This fronto-central activity might thus reflect either the inhibition of the not-to-be-given response, or the response-selection process.

3. Current technical limitations

3.1. The myth of the excellent temporal resolution of EEG/MEG: impact of averaging procedures

EEG and MEG are classically considered as methods of choice to study temporal dynamics, since their temporal resolution is excellent. However, this theoretical excellent resolution is largely degraded by the averaging process that is (currently) necessary to get an acceptable Signal/Noise ratio. Indeed, as already acknowledge more than 20 years ago by [Callaway et al., 1984] “The latency of the average is not the average of the latencies”. This is exemplified on Figure 4 that shows hypothetical single trials activities, along with their corresponding average. On the average trace, are reported both the true mean of the peaks latencies $E(X)$ and the estimated mean value, corresponding to the peak of the average. As one can see, the estimated X clearly differs from the true $E(X)$: averaging induces a temporal bias, whose exact amplitude depends on the shape of the individual traces and on their

distribution latencies. As a matter, despite its name, the averaged trace does not reflect the central tendency of the individual traces. It should be better considered the convolution of the individual shape and a probability distribution of their latencies. Such a bias precludes precise investigations of the time course of information processing.



3.2. Improving the spatial resolution of EEG and MEG to secondarily improve their temporal resolution

Because of volume conduction, the spatial resolution of conventional EEG is very low. Importantly, as clearly pointed out by [Law et al., 1993], this bad spatial resolution also induces a degradation of the temporal resolution. Indeed, since volume conduction blurs the signal, if two electrodes are located above areas activated at slightly different moment, they will both record the same blurred signal, hindering the original temporal difference (see [Vidal et al., 2003] for an example). As indicated above, some methods exist to improve the spatial resolution in the captors space, like Surface Laplacian estimation. However, if Laplacian reduces this problem, it does not eliminate it. Hence, analyzing the signal in the source space seems desirable.

4. Challenges for the future

In order to improve your estimates of spatio-temporal dynamics of information processing, three complementary directions must be followed.

4.1. Estimating the signal of interest on a trial-by-trial basis

In order to precisely estimate the time course of brain activities, averaging should be avoided. This implies that we must estimate the “signal of interest” on a trial-by-trial basis. This implies either denoising techniques [Quian-Quiroga, 2000 ; Benkherratt et al., 2005] and/or parametric estimation of the noise [Bijma et al., 2005] and of the signal in parallel.

4.2. Estimating the activity of defined regions without contamination by surrounding regions

Although powerful source localization algorithms have been developed, their use to address information processing has been quite anecdotal so far. This might come from the fact that most of those algorithms are still heavy to use (MRI of the subjects, lengthy computations etc...), making psychologists and neuroscientist not really incline to use them. Developing tools that remain compatibles with the constraints of regular psychological and/or neurophysiological experiments (large number of subject, quite a lot of conditions etc...) is necessary.

4.3. Estimating the communication between areas

As indicated in the introduction, continuous and serial models differ in the way information is transmitted from one stage to the next. It is thus necessary to measure which and how brain areas communicate. Ideally, such between areas communication should be detected on a trial-by-trial basis, to avoid the bias evoked above and to allow a better correlation with behavior.

5. Conclusions

In this brief overview, we tried to present some of the current questions in the field of cognitive neuroscience, along with the general methodology to address these questions. We have also tried to show the current technical limitations that impede more precise investigation of those issues, together with some directions to solve those technical problems.

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