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A computational neuronal model for hemispheric specialization

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Abstract: Data from neurosciences can be exploited by computer sciences to explore new models of information processing. We propose to study here hemispheric specialization and its possible underlying neuronal mechanisms. More particularly, these investigations elaborate a simple dichotomy of information processing, from parallel and spatial to sequential and temporal processing, of which we propose a neuronal implementation, based on neurobiological considerations. This is illustrated by an application, also corresponding to a task performed by human subjects in functional imaging. The usefulness of such artificial perception mechanisms for biologically-inspired robotics is also discussed.

Key-Words: Neuronal modeling, fMRI, hemispheric specialization, categorical/metric paradigm, parvo/magnocellular neurons

1 Introduction

One way to consider computational neurosciences is to model neurobiological information principles for the sake of computer sciences. Indeed, computer sciences wish to explore, better understand, formalize and implement new ways of information processing, particularly to select new interesting properties for computer-guided robotics.

New principles of information processing can arise from various domains, among which mathematics (e.g. logical calculus) and biology (e.g. genomics, neurosciences). Concerning this latter point, it is obvious that the brain has been for a long time among the best examples of information processing systems and has been of inspiration for technological domains like automation, cybernetics and computer sciences (Ballard, 1997).

Inspiration can come from structural properties. The most basic example is the distributed nature of neuronal computation (McClelland et al., 1986) and its associated properties of robustness or representation emergence, which are studied by connectionism or even by computer networking. Inspiration can also come from functional properties. Consider for example links between natural vision and computer vision (Marr, 1982). It can be clearly interesting for the latter domain to study how the former can extract such features as motion, color, orientation, etc.

Knowledge transfer from natural to technological sciences is possible through various ways, like anatomical, physiological, behavioral data and also lesional or functional imaging studies (Kosslyn et al., 1992). Conversely, modeling and simulations can bring back to neurosciences interpretations and formal frameworks to what has been studied.

This paper can be ascribed to such a reciprocal methodology. We are interested here in exploring new ways of distributed computation and at the same time in better understanding a functional property of the brain. This property, the hemispheric differentiation of the brain, is certainly among the most famous and popular in the domain. It is also one of the most unclear and controversial, though possibly at the origin of one of the most important human attribute: the language.

In the first section of the paper, we just give some evidences from neurosciences about hemispheric differentiation and concentrate on precise data and tentative theories to explain more specifically the phenomenon. On this basis, the second section presents a dual model of information processing at the same time consistent with biological data and proposing a new and powerful framework of information processing. The model is applied to a perceptual task which has also been carried out in humans within a fMRI study. Several observations of this neuroimag-

ing study can be interpreted through the characteristics of the computational neuronal model. The paper concludes on the reciprocal enrichment of the approach and proposes, for both neurosciences and computer sciences, experiments that could assess and develop this fundamental model of information processing.

2 Neurosciences point of view

2.1 Hemispheric specialization

At a macroscopic level, our two cortical (and even more generally cerebral) hemispheres can be related to perceptual and motor lateralization. For example, anatomical studies have shown for a long time that the left (resp. right) visual field projects onto the right (resp. left) occipital cortex and that the left (resp. right) hand is controlled by the right (resp. left) motor cortex.

Perhaps more interestingly, functional (and not only topological) differences have also been reported between the hemispheres. The most famous example is that of language, frequently reported to activate left cerebral areas rather than right areas, rather interested by such phenomena as prosody and other global dimensions.

Concerning vision, matching tasks have shown that large patterns are best processed by the right hemisphere and small patterns by the left one (Robertson and Lamb, 1991). Similarly, the right hemisphere seems more specialized for encoding the global shape of objects whereas the left hemisphere rather encodes details or subparts of objects (Delis et al., 1986).

Kosslyn and his colleagues have extensively worked on hemispheric specialization and have proposed a deeper and perhaps more general interpretation of it, the categorical/metric paradigm (Kosslyn et al., 1992, Kosslyn et al., 1994, Baker et al., 1999, Kosslyn, 1987). They propose that the right hemisphere best processes metric relations (absolute distances, specific shapes) whereas the left hemisphere best processes categorical relations (generic spatial relations like “on the left”, categories of shapes).

This principle has been illustrated by a famous experiment (Baciu et al., 1999) where a subject must judge whether the distance between a spot and a baseline is higher or lower than a reference distance. If the actual distance is very different from the reference distance, the answer “below” or “above” (category) can be given very quickly and the left hemisphere is involved in the task. If both distances are close, the exact, metric distance must be measured for comparison with the reference distance and the

right hemisphere is activated.

This is a very basic interpretation of the task and we will not go here into deeper details like speed of processing or transfer of learning developed in the paper (Baciu et al., 1999). We prefer to concentrate, to summarize this presentation, on the functional properties that seem to characterize the right and left hemispheres. Faced to the same information, the right hemisphere will rather encode and process its global, metric and spatial aspects and the left hemisphere its local, categorical and sequential aspects. This can be compared with language characteristics, as well as with visual scene analysis principles reported above.

2.2 Neuronal basis of hemispheric differences

If it is clearly established that there are functional differences between the two hemispheres in the human cerebral cortex, it is less clear which precise neuronal mechanisms are responsible for the differences. Apart from the above mentioned lateralization, no clear anatomical differences have been reported between the hemispheres. It is thus at the neuronal functional level that several theories have been proposed to explain functional differences detected at a more macroscopic level. Most are reported in (Kosslyn et al., 1994) and are concerned with the neuronal receptive fields. We propose here to give a brief overview of these theories.

1. (Kosslyn et al., 1992) have proposed that in the right hemisphere, receptive fields are large and overlapping and in the left hemisphere, smaller and less overlapping. Computer simulations have shown that metric/categorical properties can be obtained with such an architecture (Baker et al., 1999).

2. (Sergent, 1982) has proposed that receptive fields in the hemispheres might differ on the kind of spatial frequency they preferentially detect.

3. (Robertson and Delis, 1986) have suggested that the hemispheres could be preferentially tuned on different levels of organization: global on the right and local on the left.

4. From a physiological point of view, the above mentioned dichotomies are generally described through two kinds of neurons, parvocellular neurons (parvo = small cellular bodies, few connections, high spatial frequencies) and magnocellular neurons (magno = large cellular bodies, large connectivity, low spatial frequency). These neurons are also called X and Y neurons in non human primates (Lennie, 1998, Green, 1991). It is also interesting here to note that these kinds of neurons are also described to have different temporal properties: coincidence detectors for parvocellular neurons

and temporal integrators for magnocellular neurons (Nowak and Bullier, 1997), which can also refer to sequential and spatial aspects mentioned above.

5. In a more recent paper, (Kosslyn et al., 1994) have also given a more functional view of the problem. They have explained that wired receptive fields were not sufficient to predict all measured results and particularly those measured in tasks involving peripheral versus central vision. These differences that we will not describe here could be better explained with attentional mechanisms and with the idea that they are more flexible in the left than in the right hemisphere. It is particularly suggested that the left hemisphere could dynamically allocate, with attentional mechanisms, the most interesting size scale corresponding to the task.

Several points must be added as far as these theories are concerned. Of course, they are not exclusive, but rather partly overlapping one with the other. They were presented on a functional basis, but clearly also implicate anatomical aspects (e.g. size of receptive fields and of cellular bodies, connectivity). It can be advocated that these supposed anatomical differences are very thin and difficult to detect. Moreover, it must be underlined here that the functional hemispheric differences must be understood in terms of preferences. A specific hemisphere can be reported to perform better in some specific cases but never to be the only possible actor for these cases. On the contrary, both hemispheres are generally able (at different levels of performance) to perform any task with an appropriate training.

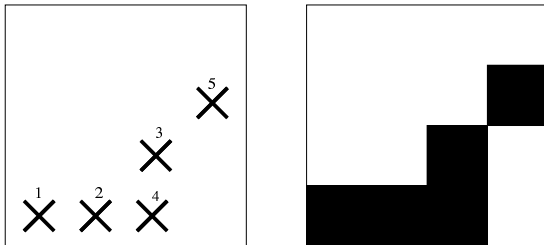


Figure 1: Metric encoding. Left: spots are presented sequentially in an empty matrix. Right: pattern presented for comparison.

We are consequently dealing here with preferences rather than with strict specializations at the functional level. Accordingly, the neuronal level must be understood as mixing the considered anatomical and functional elements. For example, parvo cellular and magnocellular neurons are present in both hemispheres, but perhaps not exactly at the same places neither in the same proportions. This is all the more difficult to investigate from a neurosciences point of view. That is also the reason why computer sciences

models can help better understanding the influence of each element because pure and extreme cases can be more easily considered in models, even if not realistic.

2.3 Functional imaging experiment

To better explore and understand these phenomena, we have proposed a multidisciplinary project, supported by the french Ministry of Research. From a neuroscience point of view, a functional imaging protocol has been developed to better characterize metric and categorical encoding (Martin, 1999). In both cases, a 4x4 matrix is presented to subjects whose gaze is fixed at the centre of the matrix. Then, a set of 5 spots are presented sequentially. Each spot appears for a short time, then disappears and after a period, the next spot appears. When the sequence of spots is entirely presented, and after a rest period, a pattern is presented in the matrix and the subject must judge if spots were presented or not at the same places. Performances and speed of answers were measured.

Now, in two parts of the experiment, two different conditions were introduced to try to force a metric or a categorical encoding (cf. figures 1 and 2). In the metric case, the matrix is completely empty and the subject must measure the absolute distance from each spot to one border of the matrix to memorize its position (cf. figure 1). In the categorical case, a grid is added and makes it easier to relate each spot in a relative way to the framework (cf. figure 2).

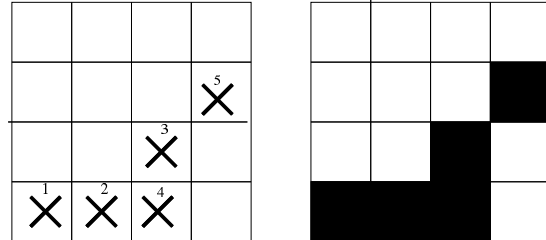


Figure 2: Categorical encoding. Left: spots are presented sequentially in a matrix with a grid. Right: pattern presented for comparison.

This task has been performed in fMRI (functional imaging) and our neuroscientist colleagues have detected, in the supposed metric case, an asymmetric activation in the right hemisphere, particularly involving parietal and frontal regions. This can be related to the hypothesis of metric encoding in the right hemisphere and also perhaps to the involvement of attentional mechanisms implemented in these associative regions.

Concerning the supposed categorical case, no clear

asymmetry has been measured. Rather, activation bilaterally concentrates in both hemispheres in occipital regions. We are now discussing with our neuroscientist colleagues to know if the task was really corresponding to a categorical case or if a more sequential task (matching with a sequence and not with a static pattern) was more adequate to this case.

We will not go into deeper details on this neurobiological experiment. In fact, we mainly mentioned it because the task chosen for human volunteers in this experiment was also chosen for the description of the metric/categorical encoding model that we have developed within the same project and that we are now presenting.

3 Our computational model

3.1 A dual neuronal mechanism

Our model is mainly based on the hypothesis that two different kinds of processing (namely spatial over a large region, resp. temporal over a small and precise region) are performed in the right (resp. left) hemisphere. This principle has been evoked above, concerning parvocellular and magnocellular neurons.

First consider magnocellular neurons (Lennie, 1998, Green, 1991). They are neurons with many connections and a large cellular body. For that latter reason, it can be considered that, to be activated, these neurons have to accumulate over a large period of time a large number of inputs. Hence, these large neurons are performing a spatial integration (Nowak and Bullier, 1997) (a spatial 'AND'). They are not precise in time because they act over a long period of time, which is not precise because it depends on many incoming events. On the contrary, it can be very precise in space because, as (Kosslyn et al., 1992) have shown, large receptive fields with a large overlapping can be more selective than small receptive fields with a smaller overlapping. Such characteristics (long and not precise constant of time, precise spatial resolution) are very interesting to perform a precise metric encoding.

Second, consider parvocellular neurons (Lennie, 1998, Green, 1991). Their receptive fields are smaller and less overlapping. Their cellular bodies are smaller and need less input to reach the threshold of activation. In a caricatural way, it is possible to imagine such a neuron with two inputs a and b and such internal parameters that the neuron activates only if, when a appears, b has to appear on a precise and fixed period of time. It can then be said that the neuron performs a sequence or a coincidence detection (Nowak and Bullier, 1997) (a temporal 'AND') over a and b . This neuronal activation means that event a is followed by event b

with known temporal parameters. Such a function (precise temporal sequencing on spatially restricted items) is very desirable to implement a categorical encoding.

Such a dual neuronal behavior can be easily implemented with a leaky integrator neuronal model, as presented in (Reiss and Taylor, 1991). This kind of temporal neuronal behavior can be modeled with differential equations (Frezza-Buet et al., 2001) or with a finite-difference equation as proposed in (Reiss and Taylor, 1991).

In that paper, the input to a neuron at time t , denoted by $I(t)$, is a continuous value ranging from zero to one. The membrane potential $A(t)$ is written as:

$$A(t + 1) = f(I).I(t) + (1 - f(I)).A(t) \quad (1)$$

where the function $f(I)$ writes, with constants a and d :

$$f(I) = d(1 - I) + aI. \quad (2)$$

The output of the neuron is computed through the Heaviside function H as:

$$Out(t + 1) = H(A(t) - 0.5) \quad (3)$$

Figure 3 shows the wave input attack in the time $1/\ln(a)$ and the wave input decay in the time $1/\ln(d)$ of neuronal activity. Given the appropriate choice of constants a and d , it is then possible to choose a very narrow activity, as for neuron A, corresponding to a categorical behavior or a more wide spreading activity, as neurons B and C, corresponding to a metric behavior. The figure also indicates that, in this latter case, overlapping of activity (and hence possible learning) is easier to obtain.

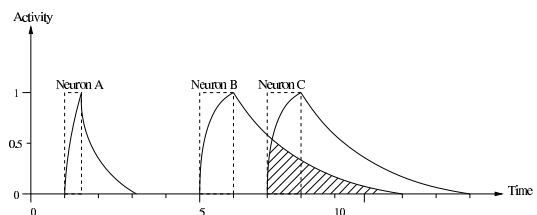


Figure 3: This figure illustrates the typical behavior of leaky integrators. It also shows the differences between a short constant of time (neuron A) and a longer, where the activity of two such neurons can more easily overlap (neurons B and C).

3.2 Experiments

We have developed a map of such neurons for our perceptual task, in both conditions. Figure 4 illustrates this mapping. The neurons are equally distributed over the perceptual surface. Of course, in

the metric case, only the matrix appears and the grid is not present. In the case of categorical encoding, the receptive fields are as large as the grid tiles. Parameters a and d are chosen to attenuate the activity during the period between two spots. In the case of metric encoding, the receptive fields correspond to the quarter of the matrix. Parameters a and d are chosen to attenuate the activity during the whole task.

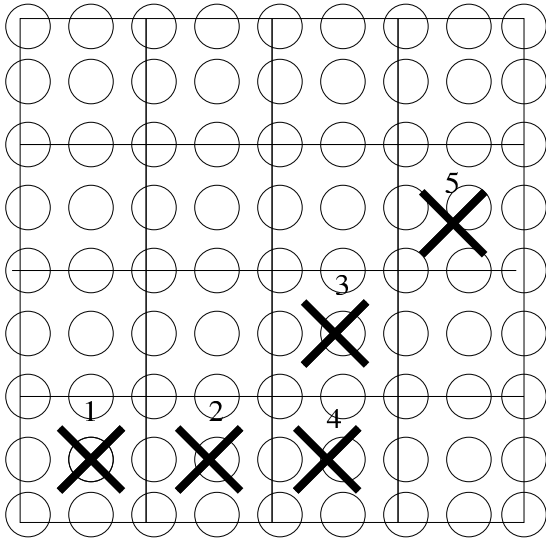


Figure 4: The mapping of a population of neurons on perceptual data. In the metric case, the grid is not present.

The neuronal input function $I(t)$ has been chosen to distinguish between the two kinds of possible inputs and to accumulate them separately, namely the static part (a part of the grid and/or a part of the matrix) and the dynamic part (a spot). Three experimental cases have been considered. In the first case (cf. figure 2), spots are presented in a grid and the pattern proposed for comparison is static. In this case, both mapping are able to encode the spots very simply. This can be related to the functional imaging task in the categorical case, where both occipital regions are active. In the second case (cf. figure 1), spots are presented in an empty matrix and the pattern proposed for comparison is static. In this case, only the metric neuronal mapping can encode the pattern, because receptive fields are too small in the categorical case. This can be related to the metric case in the functional imaging task, where the right hemisphere has a higher activity.

We have also considered another case, illustrated in figure 5. This case corresponds to the previous categorical case, except that the pattern proposed for comparison is also dynamic. The sequence of presentation (and not only the positions of the spots)

must be encoded. This was not explored during the functional imaging task, but this experiment was proposed, in our discussions with our neuroscientist colleagues, as a possible way to selectively activate the left hemisphere and really explore categorical encoding.

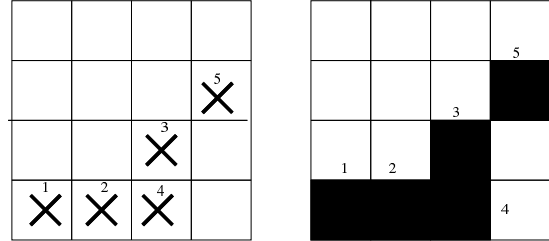


Figure 5: A more real categorical encoding. Left: spots are presented sequentially in a matrix with a grid. Right: pattern presented also sequentially for comparison.

In our computer model, this pattern can be only encoded by the categorical network, because the metric network has no sufficient temporal precision. Now, another mechanism must be evoked here. We have shown in the latter two cases that a specific distributed encoding was possible with either the categorical or the metric network. It must be now explained how the separate parts (neurons encoding a spot and its relation to a piece of the static framework) can be linked together in a global representation.

We have reported above an hypothesis by (Kosslyn et al., 1994) explaining that attentional mechanisms were responsible of such a task. We have mentioned that this could also explain an associative (parietal and frontal) activation in the corresponding hemisphere. We have explored in the past (Alexandre and Guyot, 1995) such an attentional mechanism, with the internal shift principle. Based on neurobiological consideration, this principle explains that a distributed pattern can be encoded as specific subparts articulated with the corresponding internal shifts. We have also explained in that paper (Alexandre and Guyot, 1995) that this was the function of parietal areas, associating visual patterns (corresponding to the subparts of the global pattern) with eye movements. In our hypothesis, this could correspond, in the metric case, to the association of the described mapping of neurons with the information 'no eye movement', because the receptive fields are large enough. In the categorical case, the mapping of neurons, whose receptive fields are more restricted in space, could be associated with the corresponding internal eye movement, seen as an attentional mechanism. In accordance with (Kosslyn et al., 1994), this could explain why

the left hemisphere is more efficient in dynamical attention allocation. These hypothesis are presently corresponding to ongoing model experiments.

4 Discussion

These ongoing tasks in computer sciences are also corresponding to ongoing tasks by our neuroscientist colleagues to better assess functional image interpretation in the reported cases. This is also an example of cross-fertilization between computer sciences and neurosciences in the framework of natural and artificial information processing understanding.

Other more fundamental conclusions can also be drawn from this study. They are concerned by the basic mechanism underlined here. In both natural and artificial information encoding and processing, it is obvious that global spatial and sequential temporal processing must be performed. This study underlines that they seem to be done rather separately in the hemispheres and that a very simple and dual mechanism could explain the basis of this processing and its relation to cerebral specialization within the two hemispheres.

This view is fundamental to better understand brain functioning. We also want to insist here that it can also be fundamental for technological domains like robotics or language processing. Concerning this latter point, such a sequential neuronal processing could be investigated to model language as the sequential learning of spatially restricted items (symbols?). Concerning the former point, our team is presently engaged in implementing, in real robots, life-like perception systems. This dual approach will be considered as a new and rich way of information encoding. Indeed, we can imagine how it can be useful for a robot to have at its disposal this dual encoding of its perceptual scene. On the one hand, global shapes can be precisely encoded in a metric framework, for recognition and comparison purpose. On the other hand, more local items, possibly corresponding to subparts of an object or to objects processed by other (metric) lower areas and represented in a more synthetic way, can be combined in a categorical framework, which seems more appropriate for such tasks as scene interpretation, reasoning or planning.

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