

# A new model of visual processing based on space-time coupling in the retina

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## Abstract

We propose a new model of processing and coding of visual information. The model is supported by several experimental data. It rests on a principle of spatio-temporal coupling which takes place on the retina. This means that the spatial information resulting from the projection on the retina of the image of the visual world is turned into a set of temporal wave forms through distributions of delays varying over the retinal surface. This is realized along different scales of resolution. Indeed, the signals from the photoreceptors array are sampled with increasing rates by different types of ganglion cells, each transmitting its signal into a particular delay line.

At the cortical level, this results in the propagation of output signals of neurons, vertically across successive visual areas and horizontally within each area. In this dynamic frame, lateral inhibition is interpreted in term of predictive coding. We show how it can result in some tuning properties of cortical neurons to spatial frequency and orientation.

The global spatio-temporal retinal modulation constitutes the basis of a new type of coding of visual forms, characterised by a drastic compression, since the dimension of the resulting temporal signal is one.

## 1. Introduction

We propose a new principle of processing and coding of visual information. It leads to a new model of the selectivity to spatial frequency and orientation in neurons of the visual cortex, as well as to a new model of efficient coding of visual patterns.

Among the different sensory modalities used by animals and humans to interact with their environment, vision plays a key role for it gives access to much information on the spatial layout of the external world visible from the point of observation, relevant for goal-directed actions. Visual perception has two main functions: one consists in monitoring motor actions through their visual reafference, for instance when moving the whole body or part of it; the other concerns pattern recognition. Both functions are closely associated, and have developed conjointly during phylogenesis. They have reached a high degree of complexity in the visual system of primates and humans. In particular, our recognition capacity far outstrips that of artificial vision systems as for the number of stored forms and the time to identify any of them upon a brief display (Thorpe and Imbert, 1989).

Anatomical and electrophysiological studies have shown that the visual cortex is composed of several areas (Van Essen and Maunsell, 1983). Each contains a representation more or less distorted of the visual field. Altogether, they form a network with a complex pattern of connectivity. Other major results concern the tuning of cortical neurons. The majority of neurons in the striate cortex and extra striate areas are narrowly tuned to orientation and spatial frequency. This is not the case in the

preceding structures: the retina and the lateral geniculate nucleus (LGN) (De Valois et al 1982). This selectivity agrees with results of psychophysics according to which, in first stages of the visual system, information is processed in separate parallel channels (Schiller and Logothetis, 1990). The efficiency of this kind of decomposition is yet born out by its use in mathematical and algorithmical models for computer vision, where it leads to a multi-resolution analysis of the image (Mallat 1989). However, the interactions between the different channels, and their relations to the architecture of the visual cortex remain unclear. Besides, to our knowledge, timing relations between the channels have not been fully taken into account. On the other hand, many models have been proposed to explain the selectivity to orientation in the cortex (Linsker, 1988). But, these models are also based on a description essentially spatial of the visual system.

We think that the efficiency of the visual system in term of image processing partly results from the optimum integration of the different levels of processing (Linsker, 1990). Developing some aspects of previous reflexions (Grandguillaume 1992), we intend to show the relevance of the delays originating in the retina to some characteristics of the architecture of the visual cortex and of the neuronal processing, and to the coding of visual forms.

## 2. Delayed lines in the visual system

This part concerns the spatio-temporal organization of the streams of signals running from the first stages of the visual pathway up to the cortex. We focus on two mechanisms.

### 2.1 Decomposition of the image signal along several channels

The first refers to the different parallel channels which have been identified in psychophysics, physiology and anatomy (Schiller and Logothetis, 1990). Two of these channels originate in the retina, named X and Y in the cat, and colour-opponent and broad-band in the monkey. Their properties derive of those of corresponding ganglion cells. The ganglion cells constitute the output stage of the retina, they transform amplitude-modulated signals into frequency modulated ones (sequence of spikes). In the retina, several types of cells perform parallel analog processings locally. Each class is characterised by a particular size of receptive field. Cells with different receptive field sizes sample the photoreceptors array along different scales. In accordance with the sampling principle of Shannon, their density varies in relation to the sampling rate. These different scales can be put in relation with different spatial frequencies in the signal projected onto the retina through the optics of the eye. In the Fourier plane, the sampling rate  $\Delta X$  and the spatial frequency bandwidth  $\Delta f_s$  are linked by the relation:

$$\Delta X * \Delta f_s = K, \quad K \text{ being a constant real number}$$

These retinal characteristics are present in X and Y ganglion cells: receptive fields of X cells are smaller than for Y cells which are more scattered than X cells. Besides, the conduction velocity of axons of Y cells is much higher than that of X cells: 30-40 m/sec versus 15-23 m/sec in the cat (Stone et al 1979). The mean number of spikes in output signals of X cells is also much higher than for Y ones (so the "messages" sent by X cells are longer than ones of Y cells). From the next processing stage, the corresponding channels can thus be represented as two sets of parallel delay lines, one with a short delay, the other with a long one. Short delay lines transmit short messages and have a low spatial frequency bandwidth; long delay lines transmit long messages, their bandwidth is high.

The axons of ganglion cells reach relay neurons in the lateral geniculate nucleus (LGN). In this structure, inputs of both channels are segregated within different layers. Measure of response time have shown that the temporal segregation between the two channels is kept at the output of the LGN (Stone and Hoffmann, 1971). In the cat, rise time of Y neurons of the LGN (getting inputs from Y ganglion cells of the retina) are shorter than those of X neurons (Sestokas et al 1987), so that the processing and transmission of low spatial frequencies is yet accelerated. Besides, inputs from both fast and slow channels in the LGN participate to create additional intermediate channels (Mastrorarde 1992).

Each channel is associated a delay (from the retina to the cortex). The channel number  $n$  is represented by a set  $L_n$ ,  $n \geq 2$ , of delay lines  $L_n(z)$  so that  $L_1$  corresponds to the shortest delay and the delay of  $L_n(z)$  is shorter than that of  $L_{n+1}(z)$ . The sequence of sets  $(L_n)$  with increasing delays results from sampling of the retina at decreasing rates, so that the mean density (rapported to the retinal surface) of delay lines for each set  $L_n$  increases with  $n$ . The resulting distribution of delays within each patch of the retina is discrete.

## 2.2 Spatial modulation from the geometry of the retina

For each set  $L_n$ , the value of the delay of  $L_n(z)$  (supposed above implicitly constant for each set  $L_n$ ) is modulated by spatial factors determined by the geometry of the retina. We call  $\phi$  the operator defining the distribution of delays over the retina.

Because the retinal portion of the axons of ganglion cells is not myelinated, the conduction velocity in the retina is much lower than it is in the optic nerve (average values are about 3m/sec for Y cells and 1,6 m/sec for X cells in the monkey (Gouras 1969)). Thus, the time of transmission in the retina varies continuously in function of the distance run by the axon from the position of the ganglion cell on the retina up to the optic disk (OD), the spot of the retina deprived of photoreceptors to which all the fibers converge to form the optic nerve. In fact, the latencies measured in the optic nerve (Kirk et al 1975) shows that to the distance effect is superimposed a variation of conduction velocity. We examine this last contribution first.

### a) Radial distribution of delay due to lower conduction velocity with proximity to the center of the retina.

Indeed, to the uniformly increasing trend of latencies with increasing distance to the optic disk is superimposed a maximum centered on the center of the retina.

It results from the increasing of conduction velocity with decreasing retinal excentricity. The experimental data (Kirk et al 1975) have been obtained in the cat, and to our knowledge, no data in the monkey have been published about this variation. However, we think the same relation exists in the monkey given the similar decreasing size of the soma of primate and cat retinal ganglion cells with decreasing excentricity. Indeed, large cells have axons with a large diameter, which have a higher conduction velocity than the axons of small cells.

This variation results in a distribution of delays with radial symmetry around the fovea. This can be modelled by a first order differential equation, which must be verified by  $\phi$ :

$$\partial\phi / \partial r + k * \phi = 0$$

where  $k$  is a real positive constant, and  $r$  stands for the excentricity ( $r \geq 0$ ).

### b) Effects of distance and of the differences between nasal and temporal hemi-retinas

Given the dimensions of the retina (it covers 1100mm<sup>2</sup>), and the minimal duration between two consecutive spikes (about 1ms), the range of conduction velocities in the retina should result in a desynchronization of output signals sensible over distances of about 3 mm for Y cells and 1,6 mm for X cells in the periphery; the values of these distances decreasing with proximity to the fovea.

Besides, the distance run by the axon is not the same in each hemi-retina (the retina is shared in two parts, nasal and temporal, along both sides of the vertical meridian, see fig.1).

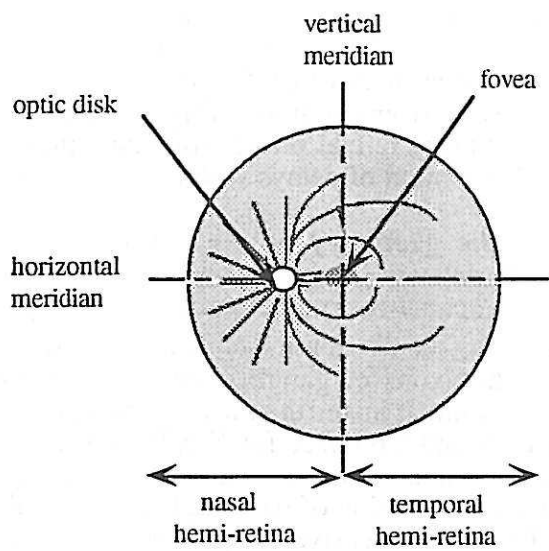


Fig. 1 - This figure shows the elements of the retinal topology and geometry relevant for the variation of delays of transmission of output signal of retinal ganglion cells in the retina. Light grey lines converging to the optic disk represent the path followed by axons in the nasal and temporal hemi-retinas.

First, the OD is in the nasal hemi-retina, about 4mm of the fovea on the horizontal meridian, making the path longer for temporal cells than for nasal cells at the same excentricity. Besides, in the nasal hemi-retina, axons converge radially up to the OD, whereas in the temporal hemi-retina they follow an arcuate path to pass round the fovea (Polyak 1941). These two different geometries not only result in different latencies or delays for signals originating at the same time in the two parts at the same excentricity, but they also result in different orientations of the gradient of delays (it must be noticed that the nasal hemi-retina of the right eye, and the temporal one of the left eye, both corresponding to the right visual hemi-field, project to the left cerebral hemisphere, and conversely for the right one).

c) Partial compensation of the increased delay of signals coming from a temporal hemi-retina

Indeed, the variation of delay between nasal and temporal hemi-retinas seems to be partly offset at the level of the optic chiasma (Bishop et al 1953), where the left and right optic nerves join to form an X (the nasal fibers crossing to go to the contralateral cortical hemisphere, while the temporal one remaining on the same side). Indeed, crossing fibers (from the nasal hemi-retinas) are added an additional length. The exact form of this compensation is unknown. Such a compensation seems logical, given the delay between input signals from right and left eyes could diverge otherwise. Rather than a point by point compensation, we suppose an almost periodic, discontinuous one, which would preserve, on 2d portions, the distinct spatial orientations of the gradients of delays from each hemi-retina.

**2.3 Propagation within the visual cortex**

The LGN is reciprocally connected to the visual cortex. In the monkey, the connections from the LGN to the visual cortex are almost exclusively limited to the striate cortex (V1). In agreement with the conservation of the different delay at the LGN output [12, 13], activation in the striate cortex has been found to spread over about 30 ms (Maunsell and Gibson, 1992).

We call  $V_n$  a visual cortical area such that  $n=1$  for the striate cortex, and the size of receptive fields of neurons of  $V_{n+1}$  is superior to that of those of  $V_n$  in the same cortical layer and at the same excentricity.  $V_n$  sends feedforward connections to  $V_{n+1}$  and possibly to other areas  $V_m$  with  $m>n+1$ , and recurrent connections to  $V_{n-1}$  for  $n\geq 2$  and possibly to other areas  $V_k$  with  $2<k<m$ . A unit  $U_{n, p, z}$  is specified by the area  $V_n$

to which it belongs, the channel  $L_p$  from which its excitatory inputs derive, and the position  $z$  of the center of its receptive field in a reference frame centered on the fovea. In the hierarchical model of the visual cortex (Van Essen and Maunsell, 1983), feed-forward information is completely processed in the area  $V_n$  before being sent to the area  $V_{n+1}$ . Besides, temporally segregated input signals are not supposed to interact within an area in which they are relayed.

We propose another interpretation of the multi-area architecture of the visual cortex. In our model, the delay lines propagate across the successive areas, so that a unit  $U_n, p, z$  is activated before a unit  $U_n, q, z$  if  $p < q$  for any area  $V_n$ , and there is a temporal overlapping between the processings of input signals from different delay lines within the successive areas. Thus, within an area, local interactions between the different delay lines are possible. These interactions can be expressed by the following relation:

$$U_n, p, z \Rightarrow U_n, q, z \quad \text{with } p < q .$$

Besides, recurrent connections can be used during the processing between the different areas, corresponding to the relation:

$$U_n, l, z \Rightarrow U_m, k, z \quad \text{with } m < n \text{ and } k < l$$

We propose that it is used to link vertically the analysis in a specific range of spatial frequency realized on each area. Indeed, analysis of low frequency components transmitted by the short delay line is completed on an area  $V_n$  with  $n \geq 2$ , in units having large receptive fields and so high positional incertitude (given we suppose the sampling principle is respected), while the analysis of high frequencies is performed in  $V_p$  with  $p < n$  (for instance  $V_1$ ) by units having smaller receptive fields (at the same eccentricity) and low positional incertitude.

The vertical propagation of signals from successive sets of delay lines is horizontally modulated within each area (according to 2.2). Dynamic processings can result from this horizontal wave form in the intra-area network, thanks to horizontal connections.

Indeed, a characteristic of the visual cortex compared to the LGN is the great number of horizontal connections, and specifically long range ones. They play a dynamic role, according to the relation:

$$U_n, q, z \Rightarrow U_n, q, z + \delta z_{n,q}$$

### 3. Cortical interaction between delayed inputs

In our model, the segregation of times of arrival of input signals on the visual cortex, coupled with lateral inhibition, results in tuning of neuronal response for different attributes of the retinal image.

#### 3.1 Predictive coding and lateral inhibition

We consider the neurons belonging to a same visual area  $V_n$ . According to part 2, some of these neurons ( $U_n, p, z$  with  $p$  and  $z$  allowed to vary separately) are activated before others. We propose that during the delay which separates times of arrival of the input signals, lateral inhibition is generated on the non-yet activated neuron from the earlier activated one. The effect of lateral inhibition is to increase the level of input activity necessary to make the neuron fire action potentials. We take the level of lateral inhibition equal to a linear function of the level of input activity of the earlier activated neuron. So, the output activity of the later activated neuron can be represented by the difference between the effective input and the predicted activity (given by lateral inhibition):

$$A_{out} = A_{in} - A_{pre} \quad (1)$$

The theory of predictive coding has been applied to represent lateral inhibition in the retina (Srinavasan et al 1982). Predictive coding is used in signal processing to compress efficiently a quantified signal, using linear prediction (the binary value of the next sample is predicted from the one of the past sample or a linear combination of past values) (Harrison 1952). The transmitted signal reflects the level of error between the effective and predictive values. One major interest of predictive coding in neural networks is that it greatly increases the dynamic range of response of the neuron, while keeping the rate of activated outputs in the network at a low level.

In our model, we suppose that convergent input signal on a unit have to be synchronous in order to produce a possible output.

### 3.2 Tuning of spatial frequency

It is based on the interaction of neurons of a same area, getting excitatory inputs deriving from different channels, and with receptive fields analysing the same part of the visual field (the receptive field of an earlier activated neuron include those of later activated ones for different channels are associated to different sampling rates on the retina). In that case, the relation (1) becomes:

$$A_{out}(U_n, q, z) = A_{in}(U_n, q, z) - A_{out}(U_n, p, z) \quad \text{with } p < q \quad (2)$$

In agreement with experimental results on the spatial frequency selectivity [4], we can represent a LGN neuron, or a ganglion cell of the retina as a low pass filter.  $f_c$  being the cut-off frequency of this filter, its transfer function can be written:

$H_{f_c}(p) = 1 / (1 + \tau * p)$  with  $f_c * \tau = \text{Cte}$ . In 2.1, we have seen that the ganglion cells of the retina process the signal in parallel, so that lower harmonics are present in the response of all types of cell. We suppose that the amplitude coding is similar between different channels, and these differ only by the value of  $f_c$ . The shorter is the delay associated to a channel, the smaller is the corresponding cut-off frequency. The relation (2) thus can be written:

$$H = H_{f_c^p} - H_{f_c^q} \quad \text{with } f_c^q < f_c^p$$

This is the difference between two low-pass filters with different cut-off frequencies. Thus the resulting form of the tuning in spatial frequencies is a band-pass filter with maximum at the frequency  $(f_c^p - f_c^q) / 2$ . This shape of tuning curve is in agreement with experimental data on cortical neurons [4]. Inhibition could be generated directly by the cortical neurons activated first or via inhibitory interneurons. In this model, the tuning curve of the early activated neurons is not modified. Neurons in the layer IV of V1 which get inputs from the LGN have such tuning curves. A possible neuronal circuit would then start from inhibitory interneurons of layer IV $\alpha$  acting on neurons situated outside the layer IV and receiving excitatory inputs from neurons in IV $\alpha$  on which partly project the intermediate and slow channels from the LGN.

### 3.3 Tuning of orientation

Pharmacological experiments have shown that reversible suppression of lateral inhibition locally in a small region of the striate cortex strongly decreases the selectivity to orientation of neurons narrowly tuned in normal conditions (Sillito 1980).

In our model, it derives from the coupling of lateral inhibition with the horizontal modulation of delays defined in 2.2. Indeed, this supposed mechanism generates a non isotropic distribution of delays between neurons of a same channel (so with separate or only partially overlapping receptive fields). The relation (1) becomes in this case:

$$A_{out}(U_n, p, z) = A_{in}(U_n, p, z) - A_{out}(U_n, p, z + dz)$$

Thus, if a spatially extended visual stimulus (like a bar shaped surface of constant color and contrast) projects over the two receptive fields, both neurons will get the same excitatory input, and the early activated will inhibit the delayed one which will remain silent. Now, rotating the bar so that it projects only on one of the two receptive-fields, excitatory inputs will differ, and the delayed neuron will not be inhibited. So, the response of the neuron is spatially oriented. Whereas delays separating inputs coming from the same hemi-retina could act only over relatively long distances, the delays separating inputs from each hemi-retina could act on very short distances.

Lateral inhibition could be produced on long range by a specific class of inhibitory interneurons. Indeed, these cells (called basket cells) have long myelinated laterally directed axons, their axonal arbors are distributed in patches far from the soma. Number of these neurons have been found in the area 18 of the cat (Matsubara et al 1987).

## 4. Implications for form recognition and object coding

We restrict here to the coding of non moving visual forms. A central issue for coding visual forms consists in finding a way of decreasing the dimension of the original signal. Several theoretical approaches based on purely spatial processing have been proposed (Haken 1991), like morphomathematics, or statistical methods.

However, the infinite diversity of visual forms makes purely spatial methods difficult to implement.

The wave-form which originates in the retina, resulting from a space-variant distribution of delays, and propagates in the visual cortex turns a purely spatial distribution of activity into a spatio-temporal one.

This process can be described as the action of time over a spatial map. The main property of time is its non reversibility (Prigogine 1980), time being considered as duration, the instant having meaning only in relation to past and future, or equivalently to the duration. The proposed principle performs a drastic reduction of dimension, since the operation consists in projecting a spatial pattern on a one dimensional axis.

Thus, each visual form projected on the retina gives rise to a specific temporal form when integrated over the whole retina, or the part on which the form projects.

The resulting coding depends primarily on the properties of the retinal spatio-temporal coupling  $\phi(z)$ . We consider that it constitutes a monotonous function, over the whole retina, or at least when restricted to a domain centered on the fovea and spreading up to a visual excentricity of about  $30^\circ$ . Besides according to 2.2, it increases from the periphery to the center of the retina. Thus, the resulting coding is coarse to fine, given the size of receptive field increases with the excentricity (2.1), for ganglion cells on the retina, as for cortical neurons of the different visual areas, at least up to V4 included (Van Essen and Maunsell, 1983). The precise form of the function can be made dependent on several factors (2.2). The properties of invariant recognition in relation to the position of the visual form in the visual field, or to specific geometrical transformations, depends in particular on this form.

To simplify, we consider here a delays distribution with radial symmetry around the fovea (corresponding to equation of 2.2 a). Figure 2 shows a simplified illustration of possible coding. It is constituted by the variations of the level of activity during the time needed to temporally scan the retinal map (or the part relevant for form recognition), from the periphery to the center. Output activities of cells with the same excentricity (i.e. same transmission delay) are summed. Thus, the number of activated cells on a circle centered on the fovea define the instantaneous level of activity. This number of activated cells depends on the geometry of the form. The form is described by the temporal variation of the level of activity, which corresponds to a chain of transitions, specified by its number of elements, the value of each one, and its position in the chain. This type of coding supports combination between forms.

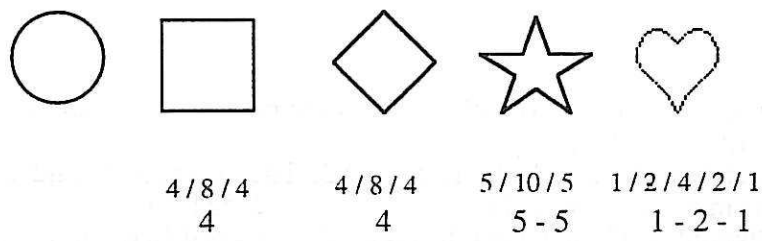


Fig. 2 - It shows an instance of simplified description of visual forms derived from the temporal form obtained for a radial distribution of delays. The center of gravity of each form is projected on the center of the retina. On the first bottom line, for each form, a sequence of figures represents the variation of the number of activated retinal cells along concentric circles centered on the fovea from the periphery to the center. This number corresponds here to the number of points of the contour of the form tangent to a circle or crossing it. A circle centered on the fovea gives rise to a single level of activity, and to no transition (left). The second line shows another representation, obtained when only points where contour curvature changes are taken into account.

In this case, there is virtually no translation invariance, whereas the coding is totally invariant to rotation, and to changing size (only when these transformations are applied to patterns projected in central vision). As for translation invariance, this is in agreement with experimental results which show that it is very low in the visual system

(O'Regan and Nazir 1990). Multi-scales coding builds up invariance properties, and particular position or translation coding gets more robust. This results from the analysis of low spatial frequencies by units having large receptive fields. These units have a large invariance in position, or translation. In particular, their activities should remain invariant during exploratory ocular movements, allowing the coding of different points of view of an object, or in term of predictive coding, how the global activity changes between several points of view.

### 5. Conclusion

Our model proposes that the distribution of delays which exists on the retina is used in the cortical processing of visual information, and in the coding of visual forms.

A possible limitation of its relevance to the visual system is the important local scatter of the latencies of output signals among ganglion cells of a same type (Kirk et al 1975). Indeed, this scatter could blur the temporal wave form, which is used in the model. However, we think that this scatter is suppressed at the level of the lateral geniculate nucleus, thanks to lateral inhibition and predictive coding.

Modelling the timing relations between inhibitory and excitatory signals, in particular as for the number of spikes involved would require to take into account the membrane and channel properties of the neurons, and to make additional hypotheses.

A next step will consist in investigating how the the proposed spatio-temporal coding could be effectively used in the infero-temporal cortex, where some neurons are selective to specific forms (Schwartz et al 1983). The processing of visual movement is also to be considered, together with linking the different forms resulting of ocular exploration of a given object (Otto et al 1992).

The proposed coding of visual patterns constitutes a new approach to form recognition and storing. It has potential applications for artificial vision systems. A simulation is prepared to try out its efficiency.

Being based on spatio-temporal coupling on the retina, it is activity dependent. In this, it is in agreement with a property of our visual perception and memory; indeed, it is very difficult to access to the exact internal visual representations of familiar faces or objects in their absence.

A central issue for coding concerns the type of representation continuous or discrete. In our spatio-temporal model, both operate conjointly.

At last, applications to other sensory systems are possible, like for instance to tactile sensing.

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