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Feed-forward contour integration in primary visual cortex based on asynchronous spike propagation.

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Most current models of visual contour integration involve iterative lateral or feedback interactions among neurons in V1 and V2. However, some forms of visual processing are too fast for such time-consuming loops. We propose a model avoiding iterative computation by using the fact that real neurons in the retina or LGN fire asynchronously, with the most activated firing first. Thus early firing V1 neurons can influence processing of their neighbors which are still integrating information from LGN. By limiting the number of spikes to one per neuron, we show that contour integration can be obtained in a purely feed-forward way.

Introduction

Visual contour integration, a modulation of V1 neuron responses by contextual influences outside their receptive field, responsible for the selective enhancement of smooth aligned contours (Fig. 1A, 1B), is thought to be mediated by lateral interactions among V1 neurons (Field et al, 1993; Kapadia et al. 1995; Gilbert et al. 1996) or feed-back inputs from V2 (Von der Heydt et al. 1984). Current models of contour integration involve iterative, recurrent lateral or feed-back projections (e.g. Shashua and Ullman, 1988; Hummel and Zucker, 1983; Yen and Finkel, 1997; Li, 1998; Heitger and Von der Heydt, 1993; Grossberg and Mingolla, 1985; Gove et al. 1995). The underlying idea behind these models is that visual inputs are computed and sent all at once, in a single step, to the primary visual cortex neurons (depending on the model, visual inputs can remain active during the following steps). These V1 neurons then calculate their activity levels, and send it, all at once, to their neighbours. The last step is then repeated until a satisfactory solution or an equilibrium state is reached (Fig. 1C).

These time-consuming mechanisms are in contradiction with psychophysical and electrophysiological studies of rapid visual categorization in man (Thorpe et al. 1996; VanRullen and Thorpe, 2000) and monkey (Fabre-Thorpe et al, 1998; Vogels, 1999). Behavioral responses in tasks where subjects have to detect a target (e.g. animal) in a briefly flashed (20 ms) natural image can be as short as 180 ms in monkey and 250 ms in man, bringing evidence that at least some forms of visual processing are so fast that it must be performed in a single feed-forward pass through the visual system, with probably no more than one spike per neuron between two successive processing stages. This leaves remarkably little time for recurrent loops or feedback to occur. One possibility is that this sort of ultra-rapid scene categorization could be performed without involving much contour integration. However, here we show that in fact, contour integration can occur very rapidly if one makes use of the fact that real neurons fire asynchronously, with the most activated neurons reaching their threshold first. This is a simple and well-known property of integrate-and-fire neurons.

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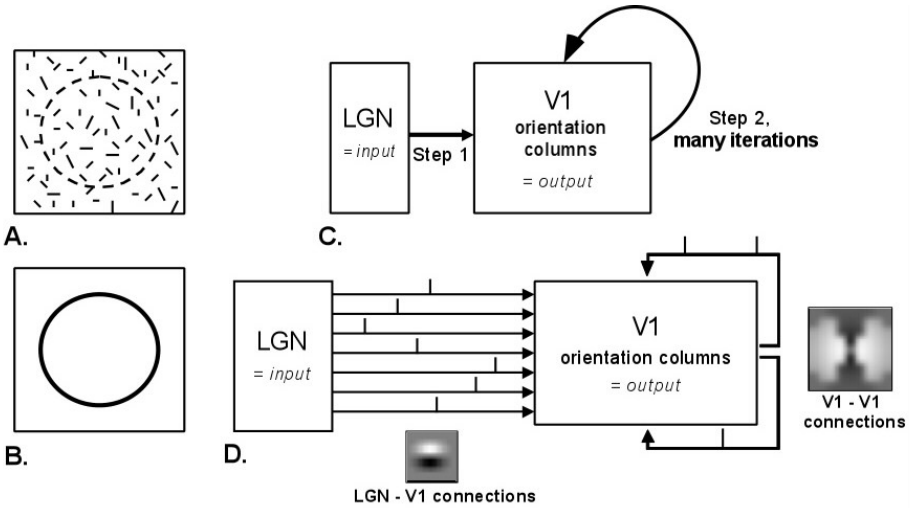

Fig. 1. Contour integration enhances the smooth contour in the retinal image A to yield to the activity pattern B in orientation columns. Classical models suppose recurrent interactions among V1 neurons (C). We propose a model based on asynchronous spike propagation where lateral interactions occur in a "feed-forward" way (D). Patterns of afferent and lateral connectivity for a V1 neuron selective to a horizontal orientation are shown.

Results

We design a two-stage model where the response of the first, input layer (which can be compared to the retina or the LGN) is a wave of asynchronously generated spikes. Neurons in the second layer, modelling the primary visual cortex V1, are selective to a particular orientation in their receptive field. In addition, they are interacting locally with one another through a set of lateral connections, similar to those proposed by Li (1998). The very first neurons to fire in V1 can start influencing the processing of their neighbors when they are still integrating the incoming information from LGN (Fig. 1D). This is compatible with electrophysiological recordings in cats (Volgushev et al. 1995) showing that the delay between the rise of PSPs in a V1 cell and the emission of its first spikes leaves enough time for lateral feed-forward interactions to occur. Neighboring neurons forming a smooth contour will receive excitatory lateral input, whereas neurons in clearly orthogonal directions will be inhibited. This lateral wave of activity modulation in V1 can spread over large distances before the end of the orientation extraction process, i.e. before the last spike has arrived from LGN. To make sure that our implementation did not permit iterations or loops in any way, we limited the number of spikes per neuron to zero or one. Orientation selectivity can still be achieved by making V1 neurons sensitive to the order in which they receive afferent spikes (Thorpe and Gautrais, 1997, 1998). Under these conditions, we were able to show for a variety of examples that contour integration indeed occured in a purely feed-forward way (Fig. 2). More specifically, we compared the activations of V1 orientation colums with and without these lateral feed-forward interactions. Activation in the retinotopic orientation maps decreased at the locations where the visual input had little or no structure, and was recruited at the locations where the contour was smooth. This was verified with artificial input images of broken lines, circles, segments, embedded in a field of random oriented bars, as well as with natural input pictures (Fig. 3).

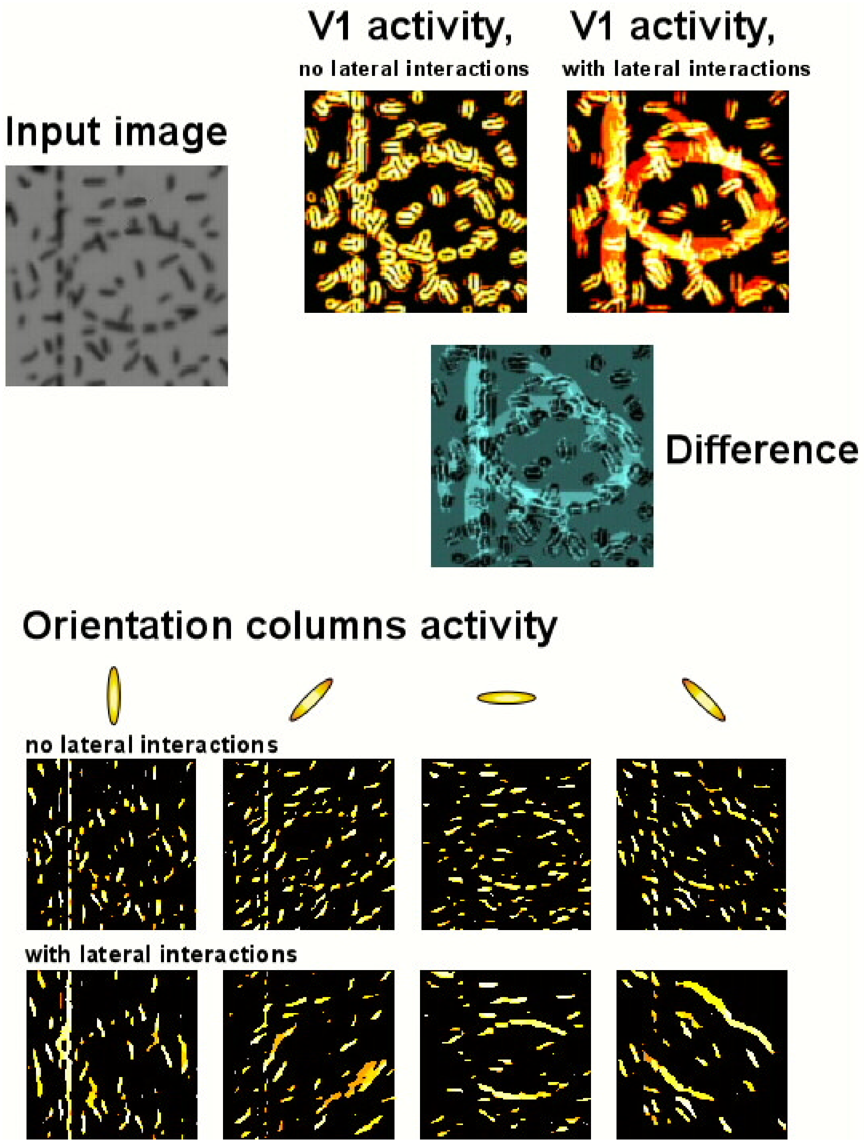

Fig 2. An example of contour integration generated by our model. The input image contains a smooth but broken contour (vertical line, oval shape) embedded in a field of random oriented bars. V1 global activities (sum of activities for 8 different orientation maps) with and without lateral interactions are shown (top). The difference image (middle) shows the regions where activity is decreased (dark spots) and the locations to where activity has moved (light spots). Activities for 4 (out of 8) orientation maps (bottom) demonstrate the selectivity of the orientation columns. These results were obtained with no more than one spike per neuron.

Discussion

The main feature of these results is that they were obtained with no iteration or computational loop, although using the same pattern of connectivity, hence the same functionality as was proposed by Li (1998) for a clearly iterative model. The major difference between these two approaches stems from the concept of information transmission and processing that we used. By simply taking into account the properties of real neurons, i.e. the fact that integrate-and-fire neurons will tend to fire asynchronously, with the most activated cells firing first, we were able to implement a visual contour integration process without any iterations.

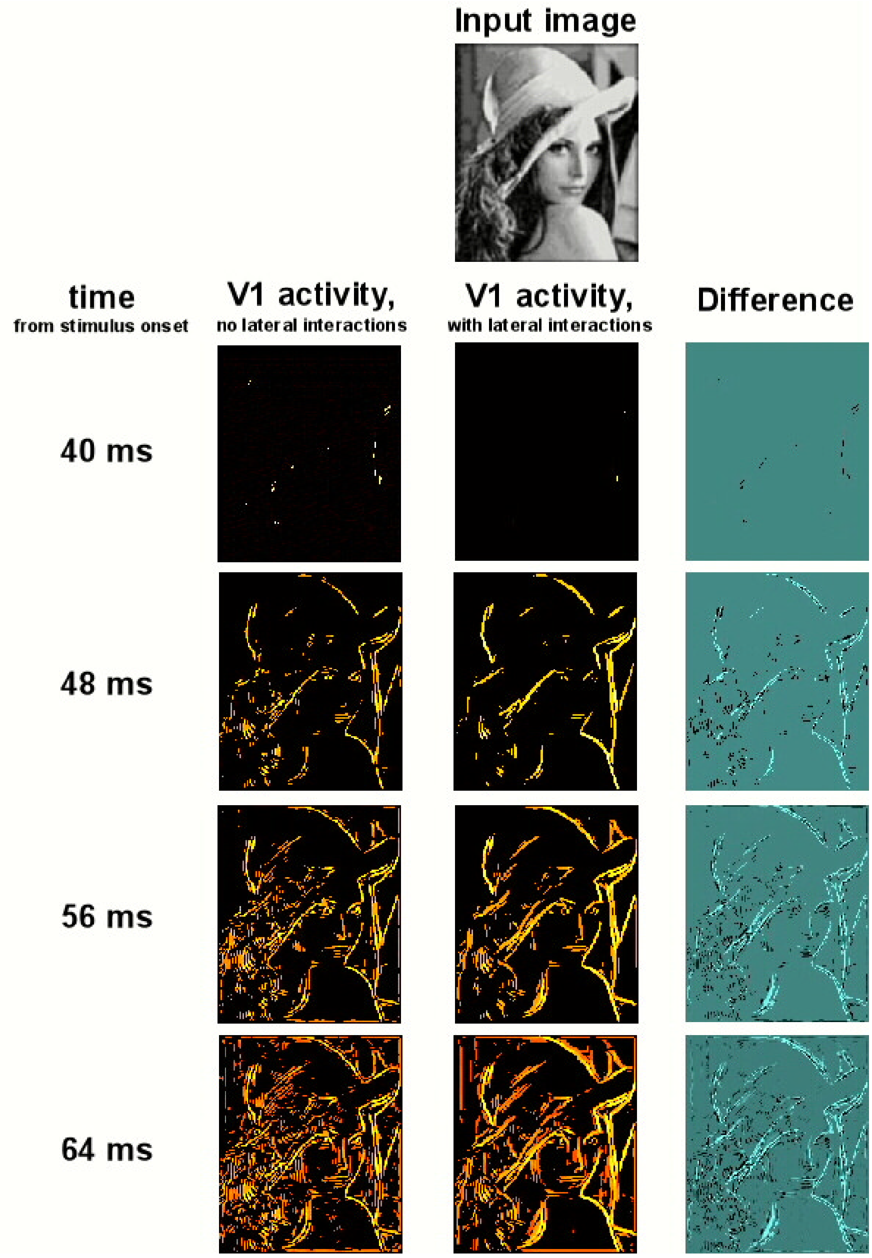

Fig. 3. Example of contour integration obtained with a natural input image. The temporal course of contour integration is simulated by assuming a uniform distribution of spikes in the retina and a 40 ms delay between the retina and V1. Lateral interactions enhance activity at smooth contours (outline of the face, shoulder, or hat), and decrease activity at locations without strong contour coherence (feathers on the hat). The effects of contour integration can be observed in the first milliseconds of processing.

We believe that many other computational mechanisms traditionally thought to involve feed-back, or recurrent lateral interactions, could be implemented in such an asynchronous feed-forward information flow framework. For example, we have already proposed (VanRullen and Thorpe, 1999) a model of feed-forward spatial attention based on the temporal precedence of the attended information under conditions where spikes are propagated asynchronously.

One could argue, on the other hand, that since our model V1 neurons are locally mutually interconnected, there is indeed some kind of recurrent processing in our model. This can not be true however, under conditions where a neuron is only allowed to generate one spike. Indeed, when a neuron fires and influences its neighbors, driving some of them above threshold, the resulting lateral interactions will have virtually no "backwards" influence on this neuron. This raises the question of how to characterize a computational loop, which is well defined in a sequential processing framework, but lacks a clear definition in the context of parallel asynchronous networks. A neural circuit can have *anatomical feedback* even under conditions where *functionally* it operates in a feed-forward mode (Treves et al, 1996). The critical issue is whether or not the circuit is able to compute the desired function even when each neuron only fires at most one spike. We suggest that the notions of iteration, loop and feedback should not depend only on the respective positions of the involved neurons in the visual cortical hierarchy, but rather on the relative time at which they respond to a visual stimulus. This is supported by recent electrophysiological studies showing that activity can occur simultaneously accross multiple hierarchically "successive" visual areas, rather than in a strictly sequential way (Bullier and Nowak, 1995).

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