



Fig. 13. A neural circuit implementing a logical/linear operator.

to activate the inhibitory interneuron when some of the conditions necessary for the operator to respond are not met. After experimenting with different configurations, a natural solution emerged by considering both the positive and negative contrast logical/linear edge operators at the same time and connecting them in a push–pull architecture that would enable each of the operators to inhibit its complement. This idea led to the circuit design shown in Fig. 13. It is pleasing to observe this interaction between the photometric characterizations at the functional level and the neuronal characterizations at the implementation level.

The circuit consists of four layer V pyramidal cells, two layer VI pyramidal cells and two inhibitory interneurons. Each of the layer V cells corresponds to a subzone of the composite receptive field. The two layer VI cells represent the responses of the two opposite logical/linear edge operators. The performance of this circuit is perhaps best described using an example. Suppose that the input to the visual field is an ideal positive contrast edge, as in Fig. 12D. Given such input, the layer V cells corresponding to the top two subzones of the receptive field (subzones 1 and 2 in Fig. 13) will burst, exciting the top layer VI cell and causing it to burst as well. At the same time, the activity of these layer V cells will also excite the left inhibitory interneuron, which will in turn inhibit the lower layer VI cell. Since, however, the layer V pyramids corresponding to the bottom half of the receptive field are inactive, the lower layer VI cell shows minimal activity regardless of the inhibition. A much more interesting case to examine is the input pattern shown in Fig. 12G. Since this is not an ideal edge, the cells monitoring the bottom half of the receptive field will burst, though with a lower frequency than the cells corresponding to the top half of the field.

Fig. 14 shows the results of our simulations. The top left of Fig. 14 corresponds to the optimal positive con-

trast edge input discussed above. As we can see, the top layer VI cell responds by bursting at a frequency much higher than baseline while the bottom layer VI pyramid shows only baseline activity.

The top right of Fig. 14 shows the results of a simulation, in which the input was a non-ideal edge such as in Fig. 12G. We simulated this by exciting the top two layer V cells with a strong current clamp ( $\approx 1.2$  mA) and injecting the bottom right layer V cell with a weaker but still substantial current clamp ( $\approx 0.8$  mA). The high frequency activity of the top two layer V cells excited the left interneuron, which in turn inhibited the bottom layer VI cell. Had the inhibition not been in place, the bottom right layer V cell would have driven the bottom layer VI pyramid to fire at a higher than baseline rate. The top layer VI cell was excited by the top layer V cells and fired at a rate substantially higher than baseline.

In the bottom left of Fig. 14, we can see the results of a simulation with input similar to the pattern in Fig. 12E. The top left and the bottom right layer V cells were injected with a strong current clamp (1.2 mA). The bottom right of Fig. 14 shows the results of stimulating all four layer V cells with a strong input (Fig. 12B).

The simulations illustrate how one cortical circuit can exhibit logical/linear-like response patterns. The compact push–pull circuit that gave the two contrasting logical/linear responses is natural and simple, and is intended as a first demonstration of concept. The effects of synaptic plasticity must also be considered in more realistic models, however, since facilitation and depression can profoundly affect the behavior of a cell. Many different types of such synapses have been found in the striate cortex, e.g., certain tufted layer V pyramidal cells that exhibit relatively fast frequency dependent depression [32].

We now show how these operators can form the basis for the curvature response; again the differences between “edge” and “line” configurations will play a key role.