situation from which the contrast difference arises untenable.

We have developed a class of non-linear local operators, called logical/linear operators [22] to confirm such conditions operationally. Subunit combinators are defined with Boolean conditions testing for the above photometric and continuity conditions. If the structural conditions are met, they return the average; if not, they veto to zero. "Edge operators" are separated from "line operators", and edge patterns from multiple curves do not combine to give an artifactual response. These nonlinearities are different from the compatibility fields above, because they are taking place at much smaller spatial scales.

We illustrate some of these cases below, but first set up the question of whether this type of non-linear response could be found in visual cortical circuits. We now illustrate one physiologically plausible possibility, beginning with the subunit interactions and then introducing the non-linearity.

The receptive fields of pyramidal neurons in layer VI are comprised of a number of zones, each of which may correspond, at least conceptually, to the receptive field of a layer V cell which synapses onto the layer VI cell. This view is supported by a Bolz and Gilbert experiment [3]: when one of the presynaptic layer V cells is pharmacologically inactivated, the layer VI cell shows no response to stimuli presented in the corresponding part of its receptive field. When the layer V neuron is reactivated, the receptive field of the layer VI cell returns to its original size.

This composite receptive field structure is a natural substrate for logical/linear operator construction. Both the tangential and the normal components consist of displaced linear operators joined together using logical/linear combinators. This is analogous to a number of layer V pyramidal cells sending axonal projections onto a layer VI neuron.

With the component construction now in place, logical/linear responses need a veto mechanism to assure no output response when at least one of the input conditions is not satisfied. Motivated by the demonstration of shunting inhibition in visual cortex [29], and after considering several possibilities in simulation, we exploit this non-linear mechanism to dramatically decrease the efficacy of excitatory post-synaptic potentials, and thereby implement the veto. In simulations we approximated shunting inhibition by decreasing the passive conductance of the cell membrane [27]. Following Borg-Graham and coworkers [29], we used a GABA type A synaptic model that was modified to increase the post-synaptic passive conductance by 200% for the duration of spiking and a short period of time ($\approx$10 ms) after each spike. This refractory period corresponded to the reuptake of the neurotransmitter and the closing of the ionic channels. Since we are working within the clique model for the columnar machine (Section 2), it is necessary for the post-synaptic conductance to remain increased between the spikes of the interneuron as it was firing at a high rate during the 3–5 spike burst. Since the soma of every cell in our model consisted of a single compartment [35], the post-synaptic conductance increase was a global change. Note that this does not make the model less realistic: the two excitatory synapses could easily be proximal to each other as well as proximal to the single inhibitory synapse.

We now illustrate the construction of a logical/linear edge operator over a receptive field with four subzones, Response to different input cases varies with the photometric configuration (Fig. 12). In cases B and C the operator should show no response due to the lack of an intensity edge. Case D is the optimal case, so the operator to respond maximally to this case. Case E should generate a weak response because only the left side of the receptive field contains the optimal stimulus. In case F, a weak response should be observed because the edge has opposite contrast. Finally, case G should generate an intermediate response due to the weak edge in the right half of the receptive field.

While shunting inhibition provides us with a useful mechanism to implement the non-linear decision step of the logical/linear operator, the tricky design issue is how

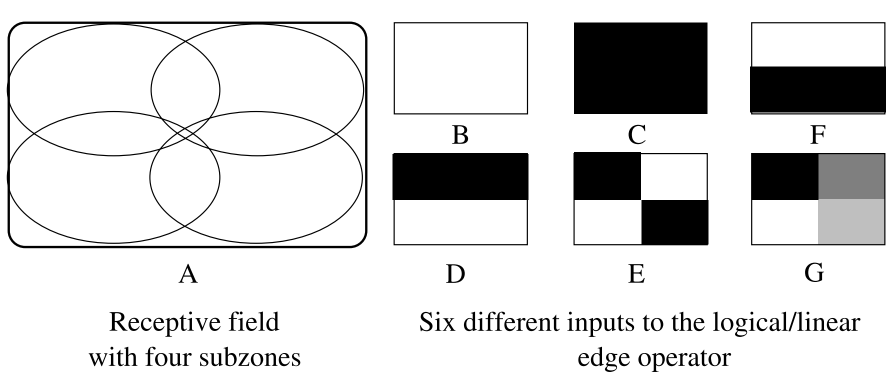

Fig. 12. Logical/linear receptive field subunits and experimental stimuli used in our simulations.