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Receptive fields and suppressive fields in the early visual system

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Fifty years of research have yielded powerful models for the responses of neurons in the mammalian early visual system. According to these models, neurons process the intensity values in visual images by performing simple arithmetic operations.

Initial models proposed that these operations are weighted sums, with weights given by a neuron's *receptive field*. These models explain the basic features of response selectivity. They were later extended to explain a number of suppressive effects originating within and outside the region of the receptive field. The resulting models rely on division. In this division, the receptive field feeds into the numerator, and the denominator is provided by a larger, non-classical *suppressive field*.

While the receptive field confers to a neuron the basic selectivity for stimulus properties, the suppressive field modulates responsiveness. A divisive suppressive field confers to neurons in early visual system a number of computational advantages. Recent evidence in higher cortical areas suggests that the modulation of divisive suppression is the primary means of operation of visual attention.

In this chapter I summarize research in receptive fields and suppressive fields in lateral geniculate nucleus (LGN) and in primary visual cortex (V1). In the following, I refer to a "suppressive field" as though this term had wide acceptance. In reality, the concept has been proposed only for LGN neurons (Levick et al., 1972), and lies forgotten since 30 years. My hope is that it will find wide acceptance to describe responses of both LGN and V1 neurons.

Receptive fields in LGN

The traditional model for responses of LGN neurons (Figure 1A) is based on a center-surround receptive field (Kuffler, 1953; Rodieck, 1965). The model takes as input a map of stimulus intensities $c(x,y,t)$ that is output by the retina. Neurons operate on this map and perform weighted sums, with weights determined by the receptive field: positive in ON regions, and negative in OFF regions. Finally, to account for the encoding of intracellular signals (which can be negative) into firing rates (which have to be positive), the model is endowed with an additional stage following summation. At its simplest, this stage performs simple rectification, i.e. it outputs zero for signals below a threshold, and is linear above this threshold (Carandini and Ferster, 2000; Granit et al., 1963).

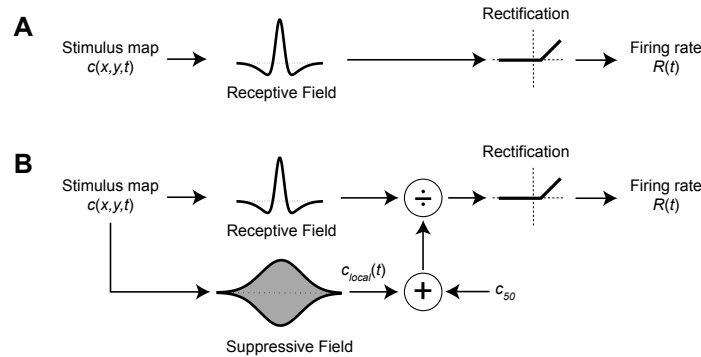


Figure 1. Two models of LGN responses. A: Model based on the receptive field. The model includes a rectification stage that converts intracellular signals into firing rate. B: Model incorporating a suppressive field and divisive gain control.

To illustrate the behavior of LGN neurons, and compare it to model predictions, I will show data from X cells of cat LGN. Most of the arguments, however, could be extended to other LGN neurons, including Y cells in cat and M and P cells in monkey.

The model based on the receptive field explains the basic features of spatial and temporal summation in LGN. For example, it explains size and the timing of the responses to drifting gratings varying in spatial frequency (Figure 2C) and in temporal frequency (Figure 2D) (Cai et al., 1997; Dawis et al., 1984). Similar results, with a similar model, have been obtained in retinal ganglion cells (Enroth-Cugell and Robson, 1984; Enroth-Cugell et al., 1983). The model can also predict responses to more complex stimuli: Full field luminance changes with rich temporal dynamics (Keat et al., 2001), and even, to some extent, complex video sequences (Dan et al., 1996).

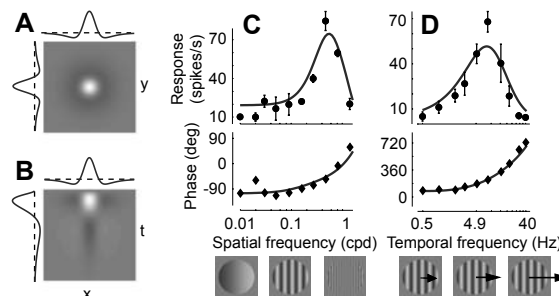


Figure 2. The receptive field of an LGN neuron explains selectivity for spatial and temporal frequency. A: Profile in space (x,y) of the receptive field of an LGN neuron (an X cell in cat LGN), described using the model by Cai et al. (1997). B: Profile in space-time (x,t) of the same receptive field. Curves illustrate corresponding one-dimensional profiles. C: Responses of the cell to drifting gratings varying in spatial frequency. Stimuli were presented in a large window and drifted at 16 Hz. Ordinates report amplitude (top) and phase (bottom) of responses measured at the stimulus frequency. Curves are predictions based on the receptive field. D: Same, for stimuli varying in temporal frequency tuning (presented at 0.7 cycles/deg). From (Mante et al., 2002).

Suppression in LGN

In addition to these behaviors, however, LGN neurons also exhibit response properties that cannot be explained by a receptive field alone. In particular, there are a number of phenomena indicating that the responses are affected by suppression originating both within and around the region of the receptive field.

A first phenomenon of suppression in LGN is contrast saturation, which can be observed with a single test drifting grating: As the contrast the grating increases, responses grow much less than proportionally (Figure 3A) (Maffei and Fiorentini, 1973; Sclar et al.,

1990). For example, the responses to 100% contrast are only about twice as large as the responses to 10% contrast, not ten times larger as predicted by the linear model based on the receptive field.

A second phenomenon of suppression in LGN is masking, which can be observed by measuring responses to the test grating in the presence of a superimposed mask grating. Both test and mask provide stimulation to the receptive field, but because their temporal frequencies are incommensurate, they elicit responses with different periodicities (Bonds, 1989; Victor and Shapley, 1980). By measuring responses synchronized to the test, one can ignore the mask's effect in driving the cell, and study its effect in suppressing responses. The latter effect is illustrated in Figure 3B,C: the mask reduces the responses to the test, and this suppression increases with increasing mask contrast (Figure 3B) and mask diameter (Figure 3C).

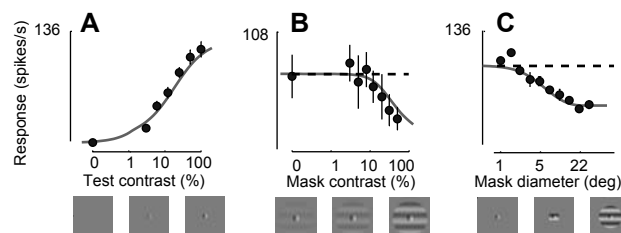


Figure 3. Saturation and suppression in an X-cell in cat LGN. A: Responses to an optimal-sized *test* grating of varying contrast. The window enclosing the grating has diameter slightly larger than the receptive field center. Responses (in this panel and the others) are measured at the test frequency (7.8 Hz). B: Effects of a superimposed orthogonal *mask* grating, as a function of mask contrast. Mask temporal frequency is 12.0 Hz, incommensurate with test temporal frequency. Test contrast is 50% (dashed line is response to test alone). C: Same, for different mask diameters. (Bonin et al., 2003b).

A third phenomenon of suppression in LGN is size tuning, which can be observed with a drifting grating of increasing size (Figure 4). If the grating has low contrast, increasing its size leads to an increase in response followed by a plateau (Figure 4, ○); This is exactly the behavior that would be expected on the basis of the cell's receptive field. If the grating has high contrast, however, increasing its size beyond an optimal value leads to dramatic decreases in response (Figure 4, ▼); This behavior is not explained by the receptive field, which would predict a scaled version of the responses to low contrast. LGN neurons, thus, are selective for size (Jones et al., 2000; Jones and Sillito, 1991; Walker et al., 1999), but only at high contrast (Bonin et al., 2002; Bonin et al., 2003a; Bonin et al., 2003b; Solomon et al., 2002).

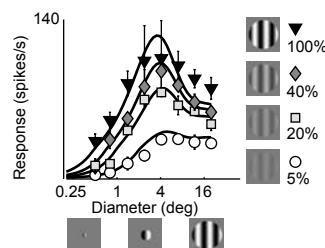


Figure 4. Selectivity for stimulus size in LGN, and its dependence on grating contrast. Responses of an X-cell to drifting gratings varying in size and contrast as indicated. *Curves* are fits of the divisive model, with parameters held fixed as obtained in Figure 3. One parameter, a responsiveness factor, was allowed to vary between data sets (Bonin et al., 2003b).

An initial wave of interest in these suppressive phenomena dates back to the 1960's. At this time it became clear that there are in LGN strong mechanisms of response reduction, as enlarging the size of disks used as visual stimuli reduced responses (e.g.

Hubel and Wiesel, 1961). Disks and bars (Cleland et al., 1983; Jones and Sillito, 1991; Murphy and Sillito, 1987), however, were inadequate stimuli to study this reduction; with such stimuli it is not clear if response reduction could be simply explained by the antagonistic surround of the receptive field or if it constituted an unexplained suppressive phenomenon. Nonetheless, these results led to fruitful studies of intrageniculate inhibition (e.g. Singer et al., 1972), and to the description of previously unknown suppressive effects (Levick et al., 1972). A key feature of these effects is that they can be caused equally by light increases and by light decreases, a behavior incompatible with a receptive field acting alone (Levick et al., 1972).

More recently, there has been renewed interest in suppressive phenomena in LGN. Experiments with drifting gratings have made it clear that selectivity for stimulus size and other suppressive phenomena arising around the region of the receptive field would not be explained by a receptive field alone (Jones et al., 2000; Solomon et al., 2002; Walker et al., 1999). Moreover, experiments with sums of gratings (test and mask, Figure 3B,C) have allowed one to measure suppression independently of stimulation (Bonin et al., 2002; Bonin et al., 2003a; Bonin et al., 2003b). We will see shortly that these experiments allow the development of a quantitative model of suppression in LGN.

Suppressive fields in LGN

To explain the suppressive effects observed in LGN, it helps to go back to an elegant paper by Levick, Cleland and Dubin (1972). These authors proposed that neurons in LGN have not only a receptive field, but also a *suppressive field*. The suppressive field is superimposed to the receptive field, and, as the term implies, its effect is suppressive. The suppressive field differs from the receptive field in two ways. First, it acts by modulating the responsiveness of the neuron, not by driving responses (for a distinction between driving inputs and modulating inputs to neurons, see Sherman and Guillery, 1998). Second, it responds to the absolute contrast of visual stimuli, regardless of their sign. While for the receptive field reversing the sign of a stimulus from dark to light would reverse the sign of the response, for the suppressive field the response is equal in both circumstances (Levick et al., 1972).

Another concept that helps understand suppressive effects is that of mechanisms of gain control (Freeman et al., 2002b; Solomon et al., 2002). These mechanisms control neuronal responsiveness, or gain, by performing division. In this division the numerator is given by the output of the receptive field, and a broader range of signals contributes to the denominator. This idea originates in earlier work aimed at explaining responses of retinal ganglion cells (Keat et al., 2001; Shapley and Victor, 1978; Victor, 1987) and of V1 neurons (Albrecht and Geisler, 1991; Carandini et al., 1999; Cavanaugh et al., 2002a; Chen et al., 2001; Heeger, 1992; Sceniak et al., 2001).

We have recently advocated a model of LGN responses that joins these disparate elements: receptive field, suppressive field, and divisive gain control (Bonin et al., 2002; Bonin et al., 2003a; Bonin et al., 2003b). In the model (Figure 1B) processing takes place not only in the receptive field, but also, in parallel, in a suppressive field. The outputs of receptive field and suppressive field feed into the numerator and denominator of a division stage. Before feeding into the denominator, however, the output of the suppressive field is added to a constant c_{50} ; This sum ensures that even at zero contrast the denominator will be larger than zero. Following the intuition of Levick and colleagues (1972), and building on research on retinal contrast gain control (Shapley and Victor, 1978; Victor, 1987), we define the output of the suppressive field to be a measure of local contrast $c_{local}(t)$, the standard deviation of the contrast map $c(x,y,t)$ in a local region

weighted by the suppressive field profile. For stimuli such as gratings and sums of gratings, local contrast is simply the square root of the sum of the square contrasts of each component grating.

This model makes excellent predictions of the responses of LGN neurons to gratings and sums of gratings (Bonin et al., 2002; 2003a; 2003b). In particular, it predicts the behaviors shown in Figure 3. The model predicts contrast saturation (Figure 3A, *curve*) because the denominator is dominated by c_{50} at low contrast and becomes noticeable at high contrast. The model explains masking because mask contrast appears in the denominator, reducing the responses to the test. In particular, the model captures how suppression increases with increasing mask contrast (Figure 3B, *curve*) and with increasing mask diameter (Figure 3C, *curve*). Some of these nonlinear effects had been previously explained with divisive models, but each effect was modeled and fitted individually (Freeman et al., 2002b; Solomon et al., 2002). Data like those in Figure 3 indicate that a divisive model can explain them all at once with a fixed set of parameters. Once these parameters are found they can be fixed, and used to predict novel data. For example, they explain the phenomenon of size tuning illustrated in Figure 4). The model correctly predicts that (as shown by Solomon et al., 2002 in macaque) cat LGN neurons are selective for size only at high contrast. Indeed, at high contrast increasing stimulus size provides a powerful signal to the denominator, substantially suppressing the responses (Figure 4, ▼). At low contrast, instead, signals in the denominator are dwarfed by the constant c_{50} , so they do not suppress responses to large stimuli (Figure 4, ○).

Origins of LGN suppressive fields

What are the origins of the suppressive field of LGN neurons? These origins certainly include retinal mechanisms of contrast gain control (Shapley and Victor, 1981; Shapley and Victor, 1978; Victor, 1987). In addition, they might include thalamic circuitry (Kaplan et al., 1987; Levick et al., 1972; Singer and Creutzfeldt, 1970; Singer et al., 1972) and feedback from primary visual cortex (Alitto and Usrey, 2003; Cudeiro and Sillito, 1996; Murphy and Sillito, 1987; Sillito et al., 1993).

An indication to the origin of suppressive signals lies in their preferences for visual attributes. A prime visual attribute in this respect is stimulus orientation, as selectivity for this attribute would strongly suggest a cortical origin. However, opinions on the matter are not unanimous: Some reports indicate that suppressive signals in LGN are selective for orientation (Cudeiro and Sillito, 1996; Sillito et al., 1993), but others suggest the opposite (Bonin et al., 2003b; Solomon et al., 2002). Additional visual attributes that have been studied include spatial frequency and temporal frequency. Signals contributing suppression are particularly responsive to low spatial frequencies and to high temporal frequencies. Because V1 neurons barely respond to low spatial frequencies (De Valois and De Valois, 1988; Maffei and Fiorentini, 1973) and to high temporal frequencies (see Freeman et al., 2002b for references), this finding is suggestive of a retinal and/or thalamic origin of the suppressive signals.

Receptive fields in V1

We now turn to primary visual cortex. We examine models that are similar to those described for LGN (Figure 1), based on receptive fields, suppressive fields, divisive gain control and rectification. As in LGN, we find that these models go a long way towards explaining visual responses of V1 neurons.

Just as in LGN, the simplest model for V1 responses is one in which neurons perform weighted sums, with weights determined by the receptive field (Hubel and Wiesel, 1959; Movshon et al., 1978b). For V1 simple cells, this model is identical to the one depicted in Figure 1A, with the difference that the receptive field would typically consist of a number of elongated ON and OFF subfields (Jones and Palmer, 1987). For V1 complex cells, moreover, the positive outputs of more than one receptive field would be summed together to yield an overall response that is insensitive to spatial position and stimulus sign (Chance et al., 1999; Emerson et al., 1992; Hubel and Wiesel, 1962; Lau et al., 2002; Movshon et al., 1978a; Spitzer and Hochstein, 1988; Szulborski and Palmer, 1990; Touryan et al., 2002). This model based on receptive field and a rectification stage explains successfully the basic features of V1 selectivity for stimulus attributes including position, spatial frequency, orientation, temporal frequency, and direction of motion (reviewed in Carandini et al., 1999; De Valois and De Valois, 1988).

Suppression in V1

As with LGN neurons, responses of V1 neurons reveal nonlinearities that require a revision of the receptive field model. In particular, these neurons exhibit clear phenomena of suppression.

First, V1 neurons receive suppression from within the receptive field (reviewed in Carandini et al., 1999; Heeger, 1992). Responses can be reduced by adding to a test stimulus a mask stimulus that might elicit little if any response when presented alone. An example of this phenomenon is cross-orientation suppression (Morrone et al., 1982), which is observed by superimposing test bars at one orientation with mask bars at a different orientation. Effective masks can have a broad range of orientations, spatial frequencies, and temporal frequencies (Allison et al., 2001; Bauman and Bonds, 1991; Bonds, 1989; DeAngelis et al., 1992; Freeman et al., 2002b; Morrone et al., 1982). Cross-orientation suppression originates in a small central region within the receptive field (DeAngelis et al., 1992).

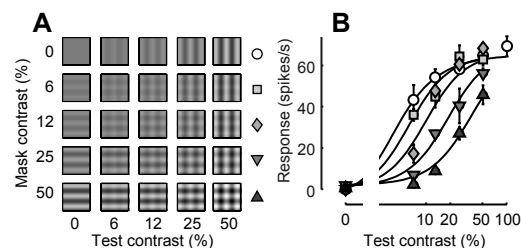


Figure 5. Cross-orientation suppression in cat V1. A: Stimuli are plaids obtained by summing orthogonal drifting gratings, the test (*top row*) and the mask (*left column*). Test and mask have same temporal frequency. B: Mean response of a simple cell as a function of test contrast. Symbols correspond to mask contrasts, from zero (\circ) to 50% (\blacktriangle). Curves indicate fits by the divisive model. Modified from (Freeman et al., 2002b).

An example of cross-orientation suppression is illustrated in Figure 5. An optimal test grating evokes a large response when presented on its own (Figure 5B, \circ), whereas an orthogonal mask typically evokes no response (Figure 5B, *leftmost data points*). Adding the mask to the test, however, substantially reduces responses: The mask shifts the curves relating response to test contrast to the right, as if it reduced the test contrast seen by the cell (Figure 5B). Because the scale of the abscissa is logarithmic, this reduction is divisive. Divisive effects of this kind have been measured in V1 of both cat (Bonds, 1989; Freeman et al., 2002b) and monkey (Carandini et al., 1997). While a similar effect is present in LGN (e.g. Figure 3B), in most LGN neurons it is weaker than

in V1 (Freeman et al., 2002b). This observation is consistent with the widely held view that cross-orientation suppression is a cortical phenomenon, i.e. it is not inherited from LGN.

Second, V1 neurons receive suppression from an area wider than the receptive field (reviewed in Fitzpatrick, 2000). Responses often decrease once a stimulus extends beyond the receptive field, and can be greatly suppressed by a mask stimulus outside the receptive field (Blakemore and Tobin, 1972; Cavanaugh et al., 2002a; Gilbert, 1977; Gulyas et al., 1987; Hubel and Wiesel, 1965; Knierim and Van Essen, 1992; Li and Li, 1994; Maffei and Fiorentini, 1976). The origins of this phenomenon might lie partially in LGN, as responses of LGN neurons are themselves subject to it (Figure 3 and Figure 4) but the effects in V1 are much stronger (Jones et al., 2000). Crucially, in V1 suppression originating from the surround is selective for orientation, being strongest when test and mask have the same orientation (Blakemore and Tobin, 1972; DeAngelis et al., 1994), and absent when they have orthogonal orientation (DeAngelis et al., 1992).

An example of surround suppression is illustrated in Figure 6. An optimal grating enclosed in a central disk evokes a large response when presented on its own (Figure 6B, \circ), whereas the same grating enclosed in a surrounding annulus evokes no response (Figure 6B, *leftmost data points*). Adding the annulus to the disk substantially reduces the responses. This effect is similar to that of cross-orientation suppression (Figure 5B).

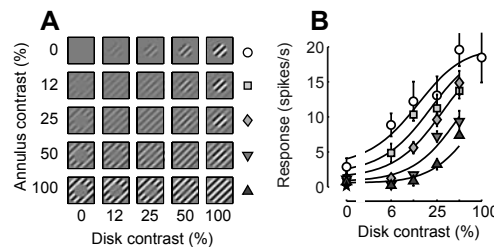


Figure 6. Surround suppression in cat V1. A: Stimuli are drifting gratings enclosed in a disk (*top row*) and in a mask (*left column*). B: Mean response of a complex cell as a function of disk contrast. Symbols correspond to annulus contrasts, from zero (\circ) to 50% (\blacktriangle). Curves indicate fits by the divisive model. From (Freeman et al., 2002a).

Suppressive fields in V1

Just as with LGN neurons, suppressive effects in V1 neurons can be explained by a suppressive field that operates divisively (Figure 1B). Such divisive models of V1 responses show great promise of explaining suppressive effects, both in the receptive field and in the surrounding region (Albrecht and Geisler, 1991; Carandini et al., 1997; Carandini et al., 1999; Cavanaugh et al., 2002a; Chen et al., 2001; Heeger, 1992; Sceniak et al., 2001). In fact, the divisive model including receptive field and suppressive field explains a number of suppression phenomena.

First, the model explains cross-orientation suppression (Albrecht and Geisler, 1991; Carandini et al., 1999; Freeman et al., 2002b; Heeger, 1992). Consider for example the data in Figure 5B. This example involves an orthogonal mask, which provides little drive to the receptive field. The mask thus contributes only to the denominator and not to the numerator of the division operation (Figure 1B), and its effect is to shift rightward the curves relating response to test contrast (Heeger, 1992). In a more general situation both gratings elicit responses when presented alone, and c_{test} and c_{mask} play a role both in the numerator and in the denominator. In this case, even though the responses are

more complicated than a simple rightward shift, a divisive model similar to the one presented here predicts them closely (Carandini et al., 1997).

Second, the model explains surround suppression (Cavanaugh et al., 2002a; Chen et al., 2001; Sceniak et al., 2001; Schwartz and Simoncelli, 2001; Solomon et al., 2002). This behavior is illustrated in Figure 6B (*curves*). Because the annulus stimulates only the fringes of the receptive field, it gives little contribution to the numerator. Nonetheless, it does contribute to the denominator, because it stimulates the suppressive field extensively.

The model also accounts for a number of additional phenomena that, just as cross-orientation suppression and surround suppression, would not be explained by the receptive field alone.

One of these phenomena is contrast saturation (Albrecht and Geisler, 1991; Heeger, 1992): At high contrasts responses grow much less than proportionally with contrast (Figure 5B, \circ , Figure 6B, \circ , Figure 7A, \blacksquare). The model explains this behavior (*curves*) because as contrast increases the output of the suppressive field goes beyond the constant c_{50} and divides the output of the receptive field by a progressively larger number. Without the suppressive field, the output of the model would have grown proportionally with contrast once above threshold.

Another of these otherwise unexplained phenomena is the selectivity for stimulus size that is observed at high contrast (Cavanaugh et al., 2002a; Kapadia et al., 1999; Sceniak et al., 2001; Sceniak et al., 1999). We have already seen this behavior in LGN neurons (Figure 4), and noted how it is explained by the divisive suppressive field. In V1 neurons, however, selectivity for size can be much more pronounced than in LGN (Jones et al., 2000). An example of this behavior is illustrated in Figure 7B, for a V1 neuron that is practically silenced by stimuli that extend beyond a critical size. For this neuron, selectivity for size appears to be present at all contrasts, but in more typical examples it is present only at high contrast, with the preferred size becoming smaller at higher contrasts (as in the LGN neuron of Figure 4). As we have already noted, the divisive model explains this behavior: Responses grow with size until the denominator becomes equal to the numerator. Then responses decrease. At higher contrasts, this point of equality—the preferred size—is achieved with smaller stimuli.

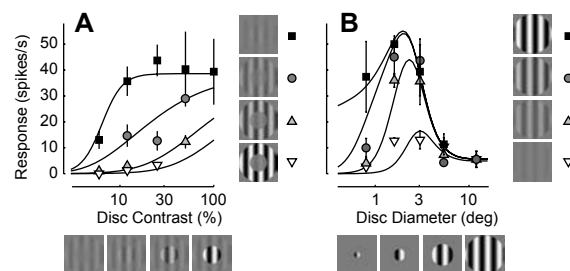


Figure 7. Responses to disks and annuli in a complex cell in cat V1. An optimal drifting grating is enclosed in a disk and an abutting annulus. Disk and annulus are abutting and centered on the receptive field. Their contrast and relative size are varied. *Curves* are predictions of the divisive model. A: Dependence of response on disk contrast for 4 annulus contrasts (disk diameter = 3 deg). B: Dependence of response on disk diameter for 4 disk contrasts (annulus contrast = 0). The disk was centered 0.7 deg away from the center of the receptive field, so for small diameters responses grow with disk diameter particularly steeply. The model was fitted to 180 responses obtained in a three-dimensional space of disk contrast, annulus contrast and disk diameter, not just to the few illustrated here. Bonin, Mante and Carandini, unpublished data.

These considerations suggest that commonly used methods are likely to lead to severe underestimation of receptive field size. Receptive field size is commonly estimated with high contrast stimuli. Because they engage the suppressive field, these stimuli make the receptive field appear smaller than it really is. To come close to mapping the receptive field faithfully, one would want to use small, low contrast stimuli. However, these stimuli elicit responses that are below threshold for spike generation, so they also lead to an underestimation of receptive field size. Only by considering the contribution of the suppressive field can one correctly estimate the size of the receptive field.

Underestimation of receptive field size might contribute to an explanation for phenomena of response enhancement resulting from remote stimulation. Indeed, there are numerous reports that regions surrounding the center of the receptive field can enhance responses (Allman et al., 1985; Kapadia et al., 1995; Nelson and Frost, 1985; Sillito et al., 1995) or cause a combination of suppression and enhancement (Jones et al., 2001; Kapadia et al., 1999; Kapadia et al., 2000; Levitt and Lund, 1996; Polat et al., 1998; Sceniak et al., 1999). These reports might become easier to understand if one considers that receptive field size is commonly 3 times larger than estimated with simple forms of stimulation (Cavanaugh et al., 2002a), so that these studies might have underestimated the area over which V1 neurons summate their inputs.

Indeed, the suppressive field explains many properties of surround suppression and enhancement, from the preference shown by surround enhancement for collinear stimuli (Polat et al., 1998), to the dependence of suppression effects on mask contrast (e.g. Levitt and Lund, 1996). The model might not explain complicated aspects of surround stimulation exhibited by some cells (e.g. Jones et al., 2002; Sillito et al., 1995), but such phenomena are not shared by a majority of cells (Cavanaugh et al., 2002b).

Finally, a contribution to response enhancement observed with remote stimulation might lie in disinhibition, i.e. the effect of suppressing the responses of mechanisms that would otherwise cause suppression (Jones et al., 2002; Walker et al., 2002). This effect is not captured by our model as it stands (Figure 1B), because in the model the suppressive field's response cannot in turn be suppressed. A feedback implementation of the model, in which the very same mechanisms that compute the suppressive field suppress each other (e.g. Carandini et al., 1997), would likely capture these effects.

Origins of V1 suppressive fields

Given that LGN neurons exhibit a suppressive field, the origin of V1 suppressive fields is likely to lie at least partially in LGN. Mechanisms of suppression in V1, however, appear to be stronger than in LGN (e.g. Bonds, 1989; Freeman et al., 2002b; Jones et al., 2000; Sclar et al., 1990). Moreover, there are clear differences between suppressive fields in LGN and V1.

A first difference between suppressive fields in LGN and V1 is that the extent of the latter depends on stimulus orientation. For stimuli that are orthogonal to the preferred orientation of a V1 neuron, the suppressive field is small, smaller than the receptive field. For stimuli parallel to the preferred orientation of the neuron, the suppressive field is large, and extends well beyond the receptive field. Indeed, suppressive signals originating in a small central region within the receptive field weigh all orientations equally (DeAngelis et al., 1992), whereas those from the surrounding region weigh orientations close to the neuron's preferred more than others (Blakemore and Tobin, 1972; DeAngelis et al., 1994; Li and Li, 1994). The peak strength of the suppressive field, however, should not depend on orientation: a small mask elicits about equal suppression at all orientations (DeAngelis et al., 1992).

A second difference between suppressive fields in V1 and in LGN lies in the spatial configuration. Suppressive fields in LGN are well described by a Gaussian envelope concentric to the receptive field (Bonin, Mante and Carandini, unpublished results). Suppressive fields of V1 neurons, instead, are asymmetric, and contain clear “hot spots” not necessarily concentric with the receptive field (Cavanaugh et al., 2002b; DeAngelis et al., 1994; Walker et al., 1999).

In summary, the suppressive field of V1 neurons is likely to be inherited from LGN only in part. Mechanisms that could contribute to suppression within V1 include feedback connections from within V1 (e.g. Carandini et al., 1997) or from higher cortical areas (e.g. Angelucci et al., 2002; Levitt and Lund, 2002).

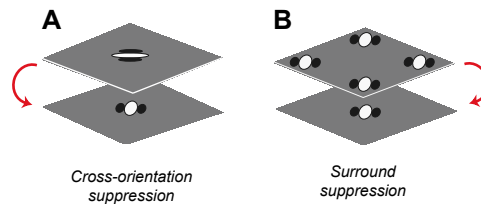


Figure 8. Interpretation of suppression phenomena in V1 in terms of intracortical inhibition. A: Cross-orientation suppression might be explained by inhibition between from V1 neurons with overlapping receptive fields and different preferred orientations. B: Surround suppression might be explained by inhibition from V1 neurons with displaced receptive fields and similar preferred orientations. Modified from (Durand et al., 2003).

In fact, the very first interpretation of suppression phenomena in V1 has been based on intracortical inhibition (Figure 8). According to this view, cross-orientation suppression would be explained by inhibition between from V1 neurons with overlapping receptive fields and different preferred orientations (Figure 8A). Likewise, surround suppression might be explained by inhibition from V1 neurons with displaced receptive fields and similar preferred orientations (Figure 8B). This intracortical explanation of suppression has been criticized (Freeman et al., 2002b), but is ingrained in current thinking about suppressive phenomena. Indeed, cross-orientation suppression was initially termed “cross-orientation inhibition” (Morrone et al., 1982).

Limitations of current models

While they promise to explain a large variety of phenomena both within and around the receptive field, current models based on suppressive fields and divisive gain control are limited in a number of ways.

First, current models are typically defined to account for suppressive effects individually. For example, a model designed to predict suppression within the receptive field is not specified to predict selectivity for size, and vice versa. Even when models are used to fit more than one data set from a given neuron, their parameters are usually not held fixed. It is thus hard to establish if a single model can explain a wide array of behaviors.

This limitation can be addressed by constraining a model with a set of measurements (as we did in Figure 3) and then freezing the parameters to test responses to other stimuli (as we did in Figure 4). Or it can be addressed by acquiring large data sets and fitting a model to the whole data set at once (as we did in Figure 7, where responses to most of the 180 stimuli are not shown for reasons of space).

Second, current models are defined only for simple, spatially localized or homogeneous, repetitive visual stimuli. Simplified visual stimuli such as bars, gratings and sums of two gratings were invaluable in allowing the development of much of our knowledge on the

early visual system. They were designed to isolate particular response mechanisms and not engage others, and to simplify (or just enable) data analysis. Thus, an essential question about current models of LGN and V1 remains open: Can they predict responses to the complex, rapidly varying visual scenes that occur outside the laboratory?

Addressing this limitation is not trivial. Visual stimuli encountered outside the laboratory tend to violate two important constraints. First, complex stimuli don't necessarily have constant mean luminance. Current models take as input a map of contrast that is output by the retina as a result of processes of light adaptation (reviewed in Shapley and Enroth-Cugell, 1984; Walraven et al., 1990). In simple stimuli such as gratings and plaids, mean luminance is constant so the retina is in an approximately constant state of adaptation, and light adaptation can be effectively ignored (Troy et al., 1999; Troy and Enroth-Cugell, 1993). In more complex stimuli, however, mean luminance can vary in space or in time, often abruptly. One must then ask: How fast is the computation of contrast? How is it influenced by luminances in recent past and local space? Second, complex stimuli are not necessarily constant for a few seconds. Divisive models of LGN and V1 are defined only for temporally stationary stimuli. In particular, the dynamics of the suppressive field contributing to the denominator have been only partially characterized.

Mechanisms of suppression

The divisive models, which I so strongly advocate, have the virtue and the fault of being abstract: With the exception of the rectification stage, which is related to spike threshold, their components do not map directly into biophysical mechanisms. In essence, these are models of the neural computations performed on images, not of the biophysical implementations of such computations. A compact description of computations performed by a neuron can then in turn guide research on the underlying biophysics.

For example, one may wonder how neurons or networks can perform an arithmetical division. There are at least two mechanisms that would yield division: shunting inhibition (Carandini and Heeger, 1994) and synaptic depression (Carandini et al., 2002). I will now describe these mechanisms, but it should be kept in mind that additional mechanisms could be at play. For example, it is possible to obtain divisive effects from subtractive inhibition from neurons whose responses grow steeply with contrast (Somers et al., 1998).

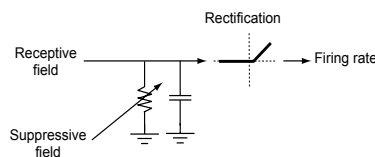


Figure 9. Divisive model based on conductance increases. The response of the receptive field is input to a simplified model of the cell membrane, a circuit composed of a resistor and a capacitor in parallel. The signals from the suppressive field control the conductance of the resistor. A rectification stage encodes the resulting signals into firing rate. Modified from (Carandini and Heeger, 1994; Carandini et al., 1997).

A first proposal for how division might be implemented in V1 was based on membrane conductance (Figure 9). We proposed that cells suppress each other's response through shunting inhibition, i.e. by increasing each other's conductance (Carandini and Heeger, 1994; Carandini et al., 1997). We argued that increasing conductance divides the contrast that is effectively seen by a neuron. Initially, this proposal has been criticized on the grounds that an increase in conductance *per se* does not necessarily have a divisive effect on firing rates (Holt and Koch, 1997). Recently, however, our view has been

supported by the discovery of a role for membrane potential noise: Increased inhibition would increase both conductance and noise, and the overall effect would be divisive (Chance et al., 2002).

We tested this model with intracellular *in vivo* measurements (Anderson et al., 2000), and found its predictions to be only partially correct. To explain cross-orientation suppression, we expected that conductance would increase markedly with contrast, and that it would not depend on orientation (Carandini et al., 1997). In a few neurons conductance did increase markedly, by about 300% (see also Borg-Graham et al., 1998; Hirsch et al., 1998; Martinez et al., 2002). Conductance increases of this magnitude, however, were only obtained with stimuli of optimal orientation, and not in all cells. If our measurements are correct (we might have been blind to conductance increases occurring in the dendrites), our proposal of conductance increases to explain cross-orientation suppression and other divisive effects will need to be revised or refined.

In fact, we recently argued that cross-orientation suppression does not result from intracortical inhibition at all (Freeman et al., 2002b). The view that cross-orientation suppression originates from inhibition is widely held (Allison et al., 2001; Bauman and Bonds, 1991; Bonds, 1989; DeAngelis et al., 1992; Heeger, 1992; Morrone et al., 1982; Sengpiel et al., 1998; Sengpiel and Blakemore, 1994; Sengpiel et al., 1995; Walker et al., 1998). However, the signals underlying cross-orientation suppression exhibit visual preferences that are hardly consistent with an intracortical origin: (1) suppression can be elicited by masks that barely evoke cortical responses, such as gratings drifting faster than about 20 Hz (Freeman et al., 2002b); (2) unlike responses of V1 neurons, signals responsible for suppression are immune to pattern adaptation, the substantial reduction in V1 responses that follows prolonged stimulation (Freeman et al., 2002b). These observations suggest that to explain cross-orientation suppression the signals providing input to the denominator in the divisive model should originate in LGN and not in cortex.

We searched for another mechanism that causes division, one that would carry signals from LGN to the denominator of V1 neurons. We found a promising candidate in synaptic depression (Carandini et al., 2002; Freeman et al., 2002b).

Depression is a promising candidate because a single depressing synapse displays both saturation and divisive suppression (Figure 10A). Consider the responses to injection of a sinusoidal current; Depression causes a substantial saturation in response amplitude (Figure 10A, ●) (Abbott et al., 1997; Kayser et al., 2001; Tsodyks and Markram, 1997). Adding noise to the injected current (Figure 10A, ○) increases synaptic depression. The noise partially suppresses the responses to the sinusoidal current; This suppression is divisive (Figure 10A, ○, rightward shift on the logarithmic scale), as if the noise had divided the amplitudes of the injected sinusoidal current (Carandini et al., 2002).

To explore the degree to which depression can explain visual properties of V1 neurons, we included it in a classical model of a simple cell (Hubel and Wiesel, 1962). In the model, orientation selectivity (Figure 10D,E) is determined by the spatial pattern of LGN inputs, with ON and OFF subregions of the receptive field (Figure 10B) being driven by excitation from ON-center and OFF-center LGN neurons (Alonso et al., 2001; Reid and Alonso, 1995) (Figure 10C). Excitation by ON-center neurons is matched by inhibition by OFF-center neurons, and vice versa (reviewed in Hirsch, 2003). Synaptic depression, in turn, produces cross-orientation suppression: The response to the plaid (Figure 10F) is smaller than the response to test alone (Figure 10D). The model correctly predicts that the effects of suppression are divisive: Increasing mask contrast shifts to the right curves relating response to test contrast (Figure 10G). This behavior resembles that shown by

real V1 neurons (Figure 5C). We have studied model predictions for a variety of stimuli, and we have found them to capture a wide variety of effects (Carandini et al., 2002).

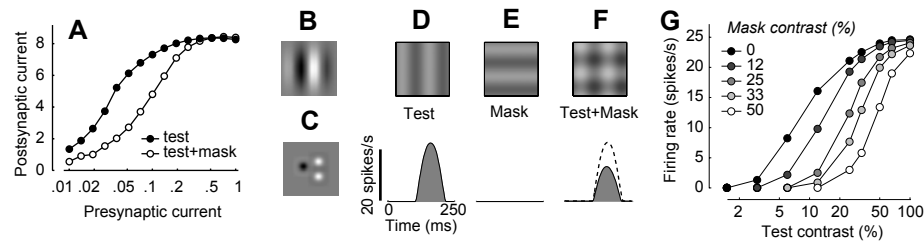


Figure 10. Modeling suppression with synaptic depression. A: Saturation and suppression in a model depressing synapse. A 2 Hz sinusoidal test current is injected into the presynaptic neuron, and the response is measured by the 2 Hz component of the postsynaptic potential (●). This response is reduced (○) when a mask current (white noise) is added to the test current. B-G: Cross-orientation suppression explained by thalamocortical synaptic depression. B: Receptive field of a model V1 neuron. C: Receptive fields of 3 model LGN neurons. D-F: Firing rate in response to gratings and plaids drifting at 4 Hz. Average response to a stimulus cycle. Stimuli are a vertical grating (D), a horizontal grating (E), and the plaid obtained by summing the two (F). *Dashed curve* is response to plaid in the absence of synaptic depression. G: First harmonic (4 Hz) of firing rate as a function of test contrast, for different mask contrasts. From (Carandini et al., 2002; Freeman et al., 2002b).

Synaptic depression would not explain suppression originating from outside the receptive field. In fact, even though both suppression within and around the receptive field are explained by a divisive model, they might not share a single biophysical mechanism. For one, these two forms of suppression have very distinct visual preferences. For example, cross-orientation suppression can be obtained with masks of all orientations (DeAngelis et al., 1992), whereas surround suppression is strongest when the mask has the preferred orientation of the neuron (DeAngelis et al., 1994). So it is possible that the two forms of suppression originate from distinct biophysical mechanisms (Carandini et al., 2002; Sengpiel et al., 1998).

Advantages of suppression

In summary, even though their biophysical implementation is not clear, divisive models including a suppressive field represent a major improvement over models based on the receptive field alone. These models have the potential to explain a wide variety of suppressive phenomena.

We expect these phenomena to play an important role in responses to complex visual scenes. We have seen that a model that ignored suppression would fare badly in predicting responses, both in LGN (Figure 3 and Figure 4) and in V1 (Figure 5, Figure 6, and Figure 7). It is hard to imagine that it would fare much better in predicting responses to more natural stimuli. Indeed, in natural images similar stimuli arise often, as the overlap of different orientations is extremely common (Schwartz and Simoncelli, 2001).

This brings us to a final question: What are the advantages conferred by a divisive suppressive field? It is hard to answer to this question, because we know little of how signals in LGN and V1 are used by subsequent stages of visual processing to yield sensation and perception. As a result, we know little of how any computation in LGN and V1 can be advantageous to later stages. There are, nonetheless, a few suggestions that have been made and might be of relevance.

A first suggestion is that a divisive suppressive field would be needed to compress the range of responses without compromising the basic output of the receptive field (Heeger, 1992). In particular, a divisive suppressive field maintains a desirable property of

receptive field outputs: That the ratio of the outputs of two neurons is largely independent of stimulus contrast (Heeger, 1992).

A second suggestion relies on a principle of optimality that has been suggested for neurons of the cerebral cortex: That they should strive to maintain statistical independence in their responses (Barlow and Földiák, 1989). It has been argued that divisive suppression of the kind shown by V1 neurons would maximize this independence (Schwartz and Simoncelli, 2001). If this is the case, evidence for divisive suppression being active already at the level of retina and LGN would suggest that the principles of statistical independence inform the responses of these subcortical structures as well.

Finally, and perhaps most interestingly to the readers of this volume, the mechanisms of divisive suppression might serve also in an eminently cognitive process, the deployment of visual attention. Considerable recent evidence suggests that visual attention enhances neuronal responses by changing neuronal gain (e.g. Fallah and Reynolds, 2001; Reynolds and Desimone, 2003; Reynolds et al., 2000) (Maunsell, this volume). It is thus conceivable that suppression and attention might engage the same mechanisms, one to obtain division, the other to obtain multiplication.

My hope is that the concept of divisive suppressive field that has evolved from research in the visual responses of LGN and V1 neurons will prove useful to understand this and other more cognitive effects of neural responses to visual stimuli.

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