Tuning Curve Shift by Attention Modulation in Cortical Neurons: a Computational Study of its Mechanisms

Physiological studies of visual attention have demonstrated that focusing attention near a visual cortical neuron's receptive field (RF) results in enhanced evoked activity and RF shift. In this work, we explored the mechanisms of attention induced RF shifts in cortical network models that receive an attentional 'spotlight'. Our main results are threefold. First, whereas a 'spotlight' input always produces toward-attention shift of the population activity profile, we found that toward-attention shifts in RFs of single cells requires multiplicative gain modulation. Secondly, in a feedforward twolayer model, focal attentional gain modulation in first-layer neurons induces RF shift in second-layer neurons downstream. In contrast to experimental observations, the feedforward model typically fails to produce RF shifts in second-layer neurons when attention is directed beyond RF boundaries. We then show that an additive spotlight input combined with a recurrent network mechanism can produce the observed RF shift. Inhibitory effects in a surround of the attentional focus accentuate this RF shift and induce RF shrinking. Thirdly, we considered interrelationship between visual selective attention and adaptation. Our analysis predicts that the RF size is enlarged (respectively reduced) by attentional signal directed near a cell's RF center in a recurrent network (resp. in a feedforward network); the opposite is true for visual adaptation. Therefore, a refined estimation of the RF size during attention and after adaptation would provide a probe to differentiate recurrent versus feedforward mechanisms for RF shifts.

Keywords: computational model, feedforward network, receptive field, recurrent network, selective attention, sensory adaptation, spotlight

Introduction

Attention is a mechanism by which the brain gates the access of sensory stimuli to its limited processing resources (Treisman and Gelade, 1980; Posner and Petersen, 1990; Desimone and Duncan, 1995). In the visual system, it has been proposed that selective attention involves a saliency map circuit (Koch and Ullman, 1985) that uses a winner-take-all strategy to select the attentional focus, and sends a 'spotlight' input to modulate activity in visual cortical areas (Treisman and Gelade, 1980; Crick, 1984; Crick and Koch, 1990; Colby, 1991; Colby and Goldberg, 1999; Vidvasagar, 1999; Gottlieb et al., 1998; Büchel and Friston, 1997; Desimone et al., 1990; Desimone, 1992; Olshausen et al., 1993; Guillery et al., 1998; Mazer and Gallant, 2003). Attention modulation of neural responses has been observed in studies with awake behaving monkeys. In extrastriate areas V4 or MT, spatial attention to a single stimulus within the receptive field (RF) of a neuron induces a moderate (Treue and Maunsell, 1996, 1999; McAdams and Maunsell, 1999; Spitzer et al., 1988) or small (Recanzone and Wurtz, 2000;

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Seidemann and Newsome, 1999; Luck *et al.*, 1997; Moran and Desimone, 1985; Motter, 1993) enhancement of firing rates (*enbancement effect*; see also Colby, 1991; Newsome, 1996; Salinas and Thier, 2000). This attentional modulation effect has been seen to correspond to an increased gain of neuronal responses, suggesting that sensory signals and attentional modulations interact multiplicatively (McAdams and Maunsell, 1999; Treue and Martínez Trujillo, 1999) at a synaptic, cellular or network level.

Connor et al. (1996, 1997) looked more closely at the spatial properties of the attentional modulation of neuronal receptive fields in area V4. They found a response gradient surrounding the attended target, as if nearby receptive fields shifted towards the attentional focus (shift effect). They also found that neuronal responses were differentially scaled as attention was directed in opposite directions around the receptive field (directionality effect). RF shift may seem to be an obvious consequence of spatial attention being mediated by a 'spotlight' bias input to the recorded cortical area. Here we show that, in fact, this is not the case. A previous attempt to explain the shift effect (McAdams and Maunsell, 1999; Maunsell and McAdams, 2001) made use of the layered feedforward architecture of the visual processing pathway. This feedforward scenario posits multiplicative scaling by attention of neurons in an early visual area (V1, V2), which project to a secondary area (V4, MT) and induce RF shift in neurons therein. This feedforward model was proposed as a scheme or word-model, but it has not been tested quantitatively. The purpose of this paper is to study a mathematical implementation of this feedforward model and to consider an alternative scenario within a single recurrent circuit receiving a focal additive excitatory input (a plausible physiological substrate for the attentional 'spotlight'). This study focuses on attention induced RF shifts, and will not deal with the directionality effect observed also by Connor et al. (1996, 1997).

It is known from psychological studies that selective attention interacts with adaptation mechanisms in the visual system (Zucker, 1990; Chaudhuri, 1990; Lankheet and Verstraten, 1995; Alais and Blake, 1999). Recent physiological work explored the effects of attention on stimuli of varying contrasts, and it was found that neuronal sensitivity to stimulus contrast is affected by attention in an inverse manner to adaptation (Reynolds *et al.*, 2000; Martinez-Trujillo and Treue, 2002).

Suggestively, experiments (Müller *et al.*, 1999; Dragoi *et al.*, 2000; Yao and Dan, 2001; Fu *et al.*, 2002; Felsen *et al.*, 2002; Kohn and Movshon, 2004) have shown that visual adaptation protocols induced tuning curve partial shifts along a variety of stimulus feature dimensions (orientation and motion direction). These observations motivated us to study both the RF shift

properties for attention and adaptation in a model network. To this end, we shall assume that adaptation occurs because of the reduction in excitability of neurons, which can be implemented as a substractive current into the neurons (Carandini and Ferster, 1997; Sanchez-Vives and McCormick, 2000; Wang *et al.*, 2003), or a negative additive 'spotlight'. We focus our modeling on the shifts in receptive field mapping of neurons in V4 (Connor *et al.*, 1996, 1997). However, attention may be focused on a stimulus feature (such as orientation or velocity), rather than location-based (Treue and Martínez Trujillo, 1999). Even though different attentional mechanisms may be involved along different stimulus dimensions (Lee *et al.*, 1997; Corbetta and Shulman, 2002), our results should apply equally well to feature-based selective attention.

Materials and Methods

We used a computational approach to explore mechanistically the involvement of the local and feedforward circuitry in the shift of the RF tuning of extrastriate neurons induced by attention (Connor *et al.*, 1996, 1997). To this end we considered two alternative scenarios: a recurrent network model and a two-layer feed-forward model.

The recurrent model is schematically represented in Figure 2*A* and presented in the Results section. It obeys the self-consistent equation

$$R(x_i) = \left[I_S(x_i) + I_A(x_i) + \frac{1}{N} \sum_{j=1}^{N} J(x_i - x_j) R(x_j) - T \right]_{+}$$

where N is the number of cells in the network; $R(x_i)$ is the steadystate firing rate of the neuron in location x_{i} T is the firing threshold of the neurons; and $[\cdot]_+$ is the thresholding operator defined as: $[I]_{+} = I$ if I > 0 and $[I]_{+} = 0$ otherwise. The sensory input is given by a truncated Gaussian function: $I_s(x) = S_0 + S_1 \exp(-0.5(x-x_s)^2/\sigma_s^2)$ if $|x - x_s| < l$, and $I_s(x) = 0$ otherwise, x_s being the position where the stimulus is presented, and *l* the spatial spread of the feedforward afferent projections. The attentional additive bias is $I_A(x) = A_1$ $\exp(-0.5(x-x_A)^2/\sigma_A^2) + A_0 \exp(-0.5(x-x_A)^2/\sigma_A'^2)$ if $|x - x_A| < l$, and $I_A(x) = 0$ otherwise, x_A being the location of the attentional focus. A_0 is either zero or negative. If A_0 is negative, $I_A(x)$ provides an inhibitory input to neurons with receptive fields peripheral to the attentional focus (assuming $\sigma'_A > \sigma_A$). Finally, the recurrent input into cell x_i is $\frac{1}{N}\sum_{i}J(x_{i}-x_{j})R(x_{j})$, where $J(x_{i}-x_{j})$ is the strength of the connection between the postsynaptic neuron at x_i and its presynaptic partner at x_i $J(x_i - x_i) = J_0 + J_1 \exp(-0.5(x_i - x_i)^2 / \sigma_I^2)$ if $|x_i - x_i| < l$, and $J(x_i - x_i) = 0$ otherwise. In all simulations shown here N = 512, T = 1, L = 4l, l = 3.14, and $\sigma_s = \sigma_I = 1.31$, $\sigma_A = 0.35$, $\sigma'_A = 0.87$, unless otherwise indicated. With this parameter choice, the unattended RF radius (half width at half height) measures 0.81, and it is larger than the attentional focus size by ~50%. The rest of parameters are typically illustrated in two different conditions: strong excitatory recurrence (Fig. 5B) and strong inhibitory recurrence (Fig. 5A). For strong excitatory recurrence: $S_0 = 0.46$, $S_1 = 0.66, A_0 = 0, A_1 = 0.089, J_0 = -2.5, and J_1 = 8.5$. For strong inhibitory recurrence: $S_0 = 0.34$, $S_1 = 1.09$, $A_0 = 0$, $A_1 = 0.28$, $J_0 = -11.9$, and $J_1 = 15.3$.

The feedforward model is represented in Figure 2B and discussed in Results. It contains two layers of neurons and their steady-state activations are described by the equations

$$\begin{cases} R(x_i) = \left[\frac{1}{N}\sum_{j=1}^{N}J(x_i - y_j)R(y_j) - T\right], \\ R(y_j) = f_A(y_j)\left[I_S(y_j) - T\right], \end{cases}$$

with $R(x_i)$ and $R(y_i)$ the firing rates of neurons in locations x_i and y_j of the second and first layers, respectively. The first layer receives the sensory input $I_5(y)$ and transduces it through neuronal input-output relationships whose slopes are modulated by the attentional signal $f_A(y) = 1 + I_A(y)$. First-layer neuronal activity is then propagated to the second layer via a fan-out feedforward connectivity profile J(x - y). The rest of symbols and functions have the same definitions as described above for the recurrent network model. The parameters used are: N = 512, L = 2l, l = 5.66, T = 0, $\sigma_S = \sigma_A = 0.21$, $\sigma_J = 0.71$, $S_0 = 0$, $S_1 = 0.42$, $J_0 = 0$, $J_1 = 6.38$, $A_0 = 0$ and $A_1 = 0.5$. With this choice of parameters tuning curves in the second layer have approximately the same tuning width than receptive fields in the recurrent model, and are ~3.5 times larger than first-layer RFs. Notice also that by choosing T = 0 and $S_0 = 0$, neurons in the first layer never use the rectification mechanism in their input-output relationships. We choose this particular case because one can then substitute $[I]_+ = I$ and this allows for precise analytical calculations (shown in the Appendix). We prove, however, that our main points regarding this model do not depend on this particular choice (see Fig. 4*C*). When we simulate an attentional signal with inhibitory surround effect, we use $\sigma'_A = 0.52$, $A_0 = -0.48$ and $A_1 = 1.5$.

For each of these models, and each parameter set explored, we found the network activity pattern in response to a single stimulus (centered at x_s), and the spatial tuning curve of a given single neuron (with RF centered at x) in response to different spatial stimuli. This is done as follows. Once the parameters for model connectivity and input stimulation are chosen, we solve self-consistently the network activity equations (Fig. 2). The solution thus obtained, the steady-state response of each neuron in the network to fixed stimulus and attentional signal, is what we call the *population activity profile* $R(x|x_s)$. We then repeat this procedure for all possible locations x_s of the stimulus signal, keeping everything else fixed. We thus obtain a family of population activity profiles $R(x,x_s)$. If we look at a single neuron (fix x, typically in our graphs x = 0 and plot its responses to different locations of the stimulus signal, we obtain the spatial tuning curve (or RF) of that given neuron at x: $R(x_S|x)$. It is this curve that we can compare to results of single unit recordings (Connor et al., 1996, 1997).

In order to quantify the effects of attention on the receptive field of a neuron, we define two quantities: the receptive field shift and the shrinking factor. Without attention, the neuron at x has a symmetric, bell-shaped receptive field and its maximum response occurs when the stimulus is presented at x. Under attention, the receptive field might shift and/or change size. In order to assess the shift of the receptive field we typically use a measure based on the location of the maximum firing in the receptive field: If in the presence of attention at location $x_A(x_A > x)$, the maximum response occurs when the stimulus peaks at $x_M \neq x$, the receptive field shift is defined as $x_M - x$, i.e. the distance in cortical space between the positions of the stimuli that elicit a maximum response when attention is present and when it is absent. When this quantity is positive (negative), the shift is towards (away from) attention. In a few cases (Fig. 4C) we also tried systematically another measure of RF shift based on a Gaussian fit to ensure that our conclusions are not dependent on the particular measure of shift used. Specifically, we fitted a Gaussian function (least-squares fit) to the RF points, but only for those firing rates that exceeded one-half of the maximum rate in the unattended tuning curve for the corresponding set of parameters. The center x_M of the fitted Gaussian was taken as the RF center and, thus, this measure of shift was defined as x_M - x. The shrinking factor is defined as the width at half height of the attended RF divided by the width at half height of the unattended RF. A shrinking factor smaller (larger) than unity indicates that the spatial tuning curve (or RF) shrinks (expands) under attention.

In all population activity profiles and spatial tuning curves shown here, only the central half of the network is plotted to avoid showing effects due to the free boundary conditions. In order to check for the robustness of the effects discussed in the recurrent network model, we carried out parameter sweeps around the values of the parameters reported. We found that any parameter could be changed by ±10%, and the qualitative results of the recurrent model in the paper would still hold. In particular, the two modes of operation illustrated in Figure 5 are robust in their qualitative features (direction of shift in neuronal RFs relative to shift in population activity profile) to a change of ± 10% in their parameters. In addition, we checked whether the shape of the input-output relationship could be critical in generating the towardsattention RF shift: we tried with the input-output function $f(I) = 2 - 2\exp\left\{-\frac{1}{2}(I - T)\right\}$ and we could still see the toward-attention shift effect for a set of parameter values very close to that reported in Figure 5B. With respect to the feedforward model simulations and calculations (see Appendix), we always used Gaussian functions for

input profiles and distance-dependent network connectivity, because they are usually seen to approximate well experimental data. However, we have checked that our results are not critically dependent on this choice: we have repeated our calculations and simulations when all curves are given by Cauchy distributions (with much longer tails than Gaussians: $1/(\alpha^2 + x^2)$) and our conclusions still hold, even quantitatively (not shown).

In addition, we have also checked that our conclusion regarding the limited range of RF shifts holds irrespective of the firing threshold used. To this end we checked the full range of threshold values that still evoke some sensory response in the first-layer network (see Fig. 4*C*). Furthermore, for the purpose of generality we have studied how dependent our conclusions are on the form of f(I) in the calculations of the Appendix: our analysis (data not shown) demonstrated that our conclusions hold qualitatively as long as cellular input-output relationships are monotonously increasing functions of the input, and under the condition that cells operate far from their strongly saturated output regime. Both of these requirements are biologically plausible and generally considered true for typical cortical neurons.

All these robustness checks point at the fact that the results reported do not require fine-tuning of parameters.

Results

Our simulations were primarily motivated by the shift effect observed by Connor *et al.* (1996, 1997). We observed that the receptive field shifts towards the attentional locus could not be reproduced as a trivial consequence of a 'spotlight' additive input. Instead, we found that the shift effect could be accounted for either by a feedforward scenario, where shifts occur as a result of upstream multiplicative scaling (as suggested by McAdams and Maunsell, 1999), or by an interplay between the attentional signal and intracortical recurrent circuitry that gives rise to a multiplicative modulation of the neural response. These two alternatives have different properties and make different predictions, which can help in teasing them apart. In order to clearly describe our results, we will first provide a heuristic argument, then show actual computer simulations from the models.

'Spotlight' Bias and Shift Effect: A Heuristic Argument

In order to clarify the challenge in explaining the shift effect (Connor et al., 1996, 1997) within a local network model where attention acts via a 'spotlight' bias input, we consider the following heuristic constructions. First, let us assume that neurons within the network do not interact with each other, their only inputs are bottom-up and top-down signals from outside the network, and their only function is to add them and transduce them into their output firing rate. We further assume that the bottom-up sensory signal and the top-down attentional signal are independent from each other, so that they carry purely stimulus and attention information, respectively. We can then plot the population activity profile for given stimuli (Fig. 1A, upper panel) and the spatial tuning curve of a single neuron for all stimuli (Fig. 1A, lower panel). In this oversimplified scenario, the attentional spotlight obviously shifts the population activity profile towards the attentional input location (Fig. 1A, upper panel). However, the receptive field of a single neuron does not show any kind of shift (Fig. 1A, lower panel). This is intuitively easy to understand: with a fixed attentional signal, when one records from a given neuron while the stimulus is varied, the attentional signal is just an additive constant on the sensory input and it does not change where the maximum of the curve occurs. This example illustrates the general point that shifts in population activity profiles usually do not carry over to spatial tuning curves (RFs of single neurons). Interactions between neurons in the network and/or between sensory and attentional signals are necessary ingredients for the shift effect reported by Connor et al. (1996, 1997) to occur in the RFs of cortical neurons.

In the following argument we dissociate two different effects in population activity profiles that might be induced by attention: pure shift and pure multiplicative scaling. In realistic scenarios (as we will consider later on) both of these effects are likely to participate in attentional modulation of the network activity. However, we can heuristically dissociate these two



Figure 1. Heuristic arguments show that shift and multiplicative scaling in the population activity profile induce opposite direction shifts in the spatial tuning curve. Each of the upper panels shows the population activity profile for three different stimulus locations (shown by the colored arrows beneath the horizontal axis). The firing activity of the neuron at location x = 0 is indicated by correspondingly colored dots. In the lower panels, the spatial tuning curve of the neuron at x = 0 is plotted (solid curve). To illustrate how this curve is built, the colored dots of the upper panels are transferred to the lower panels. The neuron's tuning curve in the absence of attentional modulation is included (dashed curve) to visualize more easily the attentional effects. Attention is always directed to neurons with receptive fields centered around a fixed location x_A , as indicated by the slender gray arrow. The structure of the mathematical expressions that were used to generate each of the three cases shown (A, B, and C) are included at the bottom. Symbols used: *R* is neuronal response, *x* is neuron label, x_S is stimulus location, x_A is attention location, I_S is sensory input current, I_A is attentional input current, 0 < f < 1 is an attentional shift factor, and f_A is an attentional shift factor, and f_A is an attentional gain modulation function. Curves in upper panels are obtained by plotting *R* versus *x* for fixed x_S , while in lower panels we plot *R* versus x_S for fixed x. (A) Assuming no recurrent and no stimulus-attention interactions, the spatial tuning curve of single neurons (lower panel, compare solid and dashed curves) does not shift at all. (*B*) If the network is such that attention. (*C*) When the effect of attention is a multiplicative scaling of the network responses, without any shift (upper panel), the spatial tuning curve of a single neuron moves towards attention. (lower panel).

effects first and then explore their interrelationship in a more realistic setting. To this end, we first consider a situation in which recurrent connections and/or stimulus-attention interactions are such that the only action of an attentional top-down signal on the population activity profile is to shift the unattended population activity profile by a fixed relative amount toward attention. If we plot population activity profiles and the spatial tuning curve for this case (Fig. 1B) we obtain that a pure shift in the population activity profile induces a shift of the spatial tuning curve in the opposite direction, i.e. away from attention. In this case, the neuron shows the maximum response when it is located at the peak of the population activity profile. This happens when the stimulus is more to the left and further away from the attentional focus than in the unattended case, and the attentional signal shifts the population activity profile to the right so that it peaks at the recorded neuron. This example provides a more striking illustration of how population activity profiles and spatial tuning curves can differ largely in their qualitative properties. The 'spotlight' bias does explain the shift in population activity profile, but it does not account by itself for the receptive field shifts observed by Connor et al. (1996, 1997).

Finally, we imagine a different scenario, where shifts are completely absent in the population activity profile and the only effect of attention is a multiplicative scaling of the profile, the modulation factor is larger when the stimulus and attentional signals are closer to each other. For now we do not need to specify the mechanisms for such a multiplicative modulation. The population activity profiles and the spatial tuning curve (Fig. 1*C*) can be plotted for this situation, and we see that spatial tuning curves now shift in the right direction (towards the attentional focus), even though the population activity profiles remain centered around the stimulus location. This observation suggests a possible role of multiplicative scaling in bringing about receptive field shifts.

To summarize, our heuristic discussions show that: (i) qualitative properties of spatial tuning curve (the experimental observable neuronal receptive fields) do not necessarily carry over to population activity profiles (which are the behaviorally relevant counterpart); (ii) either recurrent connectivity within the local network or extrinsic interactions between stimulus and attention signals to the local network, or both, are needed to account for the receptive field shifts of Connor et al. (1996); and (iii) under appropriate network interactions, the network activity can shift towards attention and/or scale multiplicatively as a result of attention, resulting in opposite effects on the direction of the neuronal RF shift. Similar arguments have been presented to link perceptual effects like the tilt effect with the contextual modifications of tuning curves of V1 neurons (Gilbert and Wiesel, 1990). We now turn to mechanistic conditions under which RF shifts might be induced by attention in cortical networks.

Recurrent versus Feedforward Cortical Architectures for RF Shifts

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There are arguably many different ways in which receptive field modulations can be generated in biologically plausible neural circuits. It is known that both recurrent circuitry, feedforward connectivity and feedback connectivity are fundamental elements of cortical information processing (Douglas and Martin, 2004), and the observed attention effect is possibly produced by a combination of these various mechanisms. However, it remains an open question as to which of these may be responsible for the RF shift effect observed in a given cortical area. To shed light on this important issue, we studied two general and contrasting scenarios from the point of view of the connectivity: in the first case the neural circuit under consideration is endowed with dense local horizontal connectivity (a recurrent network), whereas in the second case the shift is primarily induced in the course of activity propagation along multiple layers of a feedforward network. Specifically we will compare the two models depicted in Figure 2. In both models, neurons are positioned in their network according to the center of their receptive field on a line of length L.

In the recurrent model (Fig. 2*A*), only one layer of neurons is simulated, which receive additive external inputs from both the stimulus ($I_S(x)$) and the attentional control system ($I_A(x)$) and recurrent inputs dependent on the activity of neighboring neurons [according to a connectivity profile $J(x_i - x_j)$ that typically incorporates an inhibitory surround, in what is known as a Mexican Hat connectivity (Amari, 1977; Salinas and Abbott, 1996; Kang *et al.*, 2003)]. Mathematically, the firing rate of a cell with the RF center at $x_b R(x_i)$, obeys the equation displayed in Figure 2*A*.

The sensory input $I_S(x)$ and the attentional input $I_A(x)$ are given by truncated Gaussian functions (see Materials and Methods for details). Depending on the parameter values, $I_A(x)$ can include an inhibitory input to neurons with receptive fields peripheral to the attentional focus. Finally, the recurrent input that a given cell at x_i feels is a sum over all neurons in the network, $\frac{1}{N}\sum_j J(x_i - x_j)R(x_j)$, where $J(x_i - x_j)$ is the strength of the connection between the postsynaptic neuron at x_i and its presynaptic partner at x_j . This Gaussian-shaped connectivity $J(x_i - x_j)$ provides cooperative excitatory interactions between neurons nearby in cortical space (and, therefore, with overlapping receptive fields) and possibly inhibitory coupling between neurons with non-overlapping receptive fields.

The feedforward model is a formal implementation of a mechanism described by McAdams and Maunsell (1999). Its schematic representation and its defining equations are displayed in Figure 2B. We simulate two layers of neurons, one corresponding to an upstream area (V1 or V2) and the other one to a downstream area (V4). We will refer henceforth to the network representing the upstream area as first-layer network and to the one representing the downstream area as secondlayer network. In accordance with the known properties of the early visual pathway, first-layer neurons (upstream area) have smaller receptive fields than second-layer neurons (downstream area). This is accomplished by having the sensory input $I_{s}(y)$ impinge on the first layer as a narrow Gaussian, and the activity elicited in those neurons is then propagated to the second layer via a fan-out feedforward connectivity profile J(x - y) that generates much wider receptive fields. Attention enters the feedforward model as a factor $f_A(y)$ in the slope of the inputoutput relationship of first-layer neurons, and it typically affects neurons in a region commensurate with the size of the receptive field in that area, as suggested by McAdams and Maunsell (1999).

The attentional factor is given by $f_A(y) = 1 + I_A(y)$, so that attention acts in the first-layer neurons by controlling their response gain in a location-specific manner: positive attentional modulations $I_A(y)$ generate a steepening of their input-output

A Recurrent network model for RF shifts



B Feedforward network model for RF shifts



Figure 2. Schematic representation of the two model architectures analyzed and compared in relation to the attentional induction of receptive field shifts. (A) the recurrent network model consists of one population of neurons (gray circles) labeled on a line according to the location of their RF centers (x_i , i = 1, ..., N). Each neuron receives additively a sensory input $(I_S(x_i))$, a more focused attentional input $(I_A(x_i))$, and inputs from other neurons x_i in the network weighed by a Mexican Hat connectivity profile $J(x_i - x_i)$. Neurons add these inputs and transduce them into firing rate through a linear-threshold function (schematically represented within each gray circle). (B) the feedforward model consists of two layers of neurons disposed similarly to neurons in (A). Neurons in the first network receive sensory input (I_S) , and the slope of their inputoutput functions is modulated according to an attentional factor $f_A(y_i)$ that induces a gain increase in those locations where attention is being focused. The first network activity propagates to the second network through a fan-out connectivity profile $(J|x_i$ y_i)). Second-layer neurons summate all their presynaptic inputs and generate an output according to a threshold-linear function. This model does not include any crosstalk between neurons in the same network. Equations below each schematic representation give a mathematical description of the models. N is the number of cells in each network; $R(x_i)$ is the steady-state firing rate of the neuron in location x_i in the network that represents area V4; $R(y_i)$ is the steady-state firing rate of the neuron in location y_i in the first-layer network (area V1, only in panel B); T is the firing threshold of the neurons; and $[\cdot]_+$ is the thresholding operator.

relationship, whereas negative attentional modulations (typically in a surround of the attentional focus) will result in a reduced neuronal response gain. We use consistent nomenclature with the recurrent network above so that $I_3(\gamma)$, $I_4(\gamma)$ and f(x - y) are given by the truncated Gaussian functions explicited in Materials and Methods.

Parameters are chosen so that tuning curves in the second layer have approximately the same tuning width than receptive fields in the recurrent model (see Materials and Methods).

The Feedforward Model for RF Shifts

We first consider the feedforward model of Figure 2B. The feedforward model proposed by McAdams and Maunsell (1999) emphasizes the fact that the attentional input targets neurons in a cortical area such that the size of the attentional beam (as required by the task) matches the size of the targeted neurons' RFs. Confirming previous proposals (McAdams and Maunsell, 1999), we found that such a model indeed produces receptive field shifts in the downstream layer that represents area V4. When shifts are produced, the magnitude of the shifts can be quite large, if one assesses this through the maximum of the tuning curve (see Methods). Note that, by definition, maximal RF shift occurs when the tuning curve moves all the way to the location of the attentional focus. In the feedforward model, when RF shifts are observed the maximum of the tuning curve can indeed be moved close to the attention focus in the feedforward model (Fig. 3A, right panel), although in this case the tuning curve is no longer Gaussian but has a bimodal shape. Another interesting feature of this mechanism is the fact that the size of the RF (assessed as half width at half height) is reduced when attention is focused on the neuron's RF center (Fig. 3B), we will come back to this later. Both of this effects are enhanced by, but not dependent on, the presence of an inhibitory surround in the attentional beam. Thus, the feedforward model is an effective architecture for generating RF shifts in areas downstream from the area where responses are multiplicatively scaled. As we now show, however, there are limitations that make this mechanism unable on its own to replicate the data of Connor et al. (1996, 1997).

We found that, under the assumption that the attentional focus footprint (spatial size) matches the RF size of neurons in the first layer, the feedforward model is able to produce RF shifts in a second-layer neuron only when attention is focused in the vicinity of the neuron's RF center, and not beyond the RF boundary (Fig. 4A). This limit can be shown rigorously by a quantitative mathematical analysis (see the Appendix). We have checked that this result is not dependent on the value of the firing threshold in neurons of the first-layer network, nor on the method used to assess the magnitude of the RF shift (Fig. 4C). Hence, the limited range for RF shifts is an intrinsic feature of the feedforward model, not a mere consequence of choice of parameter values. In contrast, the experiments of Connor et al. (1996, 1997) showed very significant RF shifts when attention was focused outside the recorded neuron's RF. The feedforward model with attentional effects restricted to the functional size of first-layer network responses is thus incompatible with the results of Connor et al. (1996, 1997). RF shifts by away-from-RF attention in neurons of the second layer can be obtained, if one allows the attentional focus on the first layer to be considerably more widespread, and affect many more firstlayer neurons than strictly those whose RF overlaps the locus of attention (Fig. 4B). By doing this, attentional shifts can be induced when attention is focused beyond the RF boundary of a second-layer neuron, even though the peak shift is significantly reduced (compare left panels in Fig. 4A,B). Notice that



Figure 3. Population activity and receptive field modulations by attention in a feedforward two-layered network. Two situations are illustrated: receptive field shift in the second-layer neuron when attention is focused onto the flank of the neuronal preferred stimulus (A panels); and receptive field shrinkage in a neuron of the second layer when attention is allocated right on the neuronal preferred stimulus (B panels). In all panels, location of attention is indicated by upward pointing gray triangles. Population profiles are drawn for stimuli presented at location x = 0, and tuning curves correspond to neurons with RF centered at x = 0. Dashed lines depict activity in the absence of attentional modulation, while solid lines contain the effects of attention. Attentive multiplicative scaling is built into first-layer neurons (lower panels), and it is transmitted through feedforward connections to second-layer neurons (upper panels). Second-layer neuron tuning curves show a variety of attentional modulations such as towards-attention shift (panel A) and receptive field shrinkage (panel B, dotted line is a rescaling of the unattended curve to show the reduction in width at half height induced by attention). The attentional signal modulates the gain of first-layer neurons (elongated tilted arrows) and it includes an inhibitory surround with $A_0 = -0.48$ and $A_1 = 1.5.$

these small peak shifts are within the range of experimental values (Connor *et al.*, 1997; see Fig. A1). However, it remains necessary in all cases to have very strong attentional modulations (>50%) in first-layer neurons.

Receptive Field Shift in a Recurrent 'Spotlight' Network Model

We have shown that to produce a toward-attention RF shift in the original feedforward network (with the attentional footprint commensurate with first-layer neurons' RF), attention needs to be focused well within the radius of a downstream neuron's RF (in contrast with the results of Connor *et al.* (1996, 1997)). This feedforward mechanism can only replicate the observations in area V4 by Connor *et al.* (1996, 1997) if one assumes that attentional modulation in the upstream area (V1) is strong and has a very broad footprint, of the size of RFs in the downstream area (V4). Although there is no conclusive evidence ruling out a broad attentional beam in V1, attentional modulations in V1 are reportedly very weak at the neuronal level. Therefore, we now turn to analyzing whether mechanisms intrinsic to a local network can generate RF shifts on their own. Our candidate mechanism is reverberatory interactions within the local circuit.

What recurrent circuitry mechanisms can implement the attentional shift effect in the local network? To address this question we considered a model of a cortical module of neurons in area V4 which have different receptive fields but the same stimulus selectivity (orientation, spatial frequency, etc.). The network model consists of recurrently connected firing rate neurons ordered along a line according to the center of their receptive fields. Recurrent connections are strongest between neighboring neurons and the network receives two types of external input: a topographic stimulus signal, and a topographic 'spotlight' attentional bias input which is spatially more focused than the stimulus input (see Fig. 2A and Materials and Methods for details). Interestingly, if recurrent connections are purely inhibitory (light gray and squares in Fig. 5C, left panel), the receptive fields shift away from the attentional focus (Fig. 5A, bottom panel). By contrast, if recurrent excitation is strong (black and circles in Fig. 5C, left panel), the RFs shift towards the attentional focus (Fig. 5B, bottom panel). Under these two different operational regimes, the recurrent connections within the network determine different ways in which the attention signal modulates the population activity profile. Thus, in one case attention induces an important shift towards attention in the population activity profile (Fig. 5A, upper panel), while in the other case it mostly results in a multiplicative scaling of the network activity without significant spatial shift (Fig. 5B, upper panel). Strong recurrent excitatory connections favor the multiplicative effect, hence a receptive field shift towards attention (see Fig. 1). As shown in Figure 5C, a gradual increase in the overall excitatory coupling of the network leads to a transition from away-from-attention shift (data in light gray and squares) to towards-attention-shift (data in black and circles).

Therefore, local recurrent circuitry can account by itself for the shift effect observed by Connors *et al.* (1996, 1997) provided the internal circuitry of extrastriate cortex operates in the regime with sufficiently strong recurrent excitatory connections illustrated in Figure 5*B* rather than that of Figure 5*A*.

In Figure 6 we simulate the Connor's experiment using the same parameters as Figure 5*B*, except with the attentional focus well outside of the neuron's RF. In close similarity with the single unit recording data of Connor *et al.* (1997) (compare with their fig. 2), in response to five stimuli presented in the receptive field, the neural activity is shifted towards the attentional signal, and the maximum response is slightly enhanced compared to the unattended case. These results suggest that the observed receptive field shift in V4 neurons can be accounted for if the underlying local circuit is endowed with sufficient recurrent connections to operate in the multiplicative regime of Figure 5*B*.



Figure 4. In the feedforward model, the footprint of attentional modulations in the first network determines whether attention focused outside the receptive field of second-layer neurons is able to induce significant RF shifts. (*A*) When the attention focus has a size comparable to first-layer neurons' RFs, no RF shifts are observed in the second-layer neurons if attention is focused beyond RF boundaries (parameters as in Materials and Methods). (*B*) when the attention focus is broad (σ_A tripled with respect to *A*) and impinges on many more neurons than encompassed in a typical first-layer neuron's RF, the feedforward model produces shifts for attention focused beyond the boundaries of second-layer neurons' RFs. Left panels: RF shifts in absolute units versus the distance between the attention focus and RF center, normalized to the RF half width at half height. Right panels: RF of a second-layer neuron in the unattended case (thin dashed line), and with attention located at two different positions within the RF (in gray and black, respectively). Area in gray indicates the extent of the receptive field (unattended RF width at half height). In (*A*), shifts disappear when the attention focus is on the border of the RF and beyond, while in (*B*) shifts persist even when attention is half a RF radius away from the RF boundary. (*C*) The limitation of the feedforward model to produce RF shifts when attention is foused beyond the neuron's RF is not dependent on the neuronal nonlinear responses, nor on the method uses to dasses the degree of shift in the RF. Left: magnitude of RF shifts in away from the first-layer neurons (Thr = 0 corresponds to the curve in panel *A*, left). Right: same as left, but RF shift is now quantified not in terms of the location of the RF peak (as in all other panels here), but the center of the Gaussian fit to the response in the second-layer neuron (see Materials and Methods). In both cases, the range of locations where an attentional focus is able to generate RF shifts remains c

Sbift and Shrinking Effects through Attentional Surround Inhibition

Figure 5 shows that a recurrent network in an appropriate operational regime can generate the receptive field shift towards attention in a 'spotlight' single recurrent network model. However, the receptive field shifts thus obtained are relatively small (see Fig. 5*B*). So, we asked under what conditions the receptive field shift is maximal. We found that the maximal shift occurs if the attentional signal contains a surround inhibitory component, i.e. when the attentional input excites neurons with receptive field near the attentional

locus but it inhibits neurons with receptive fields peripheral to the attentional focus (Fig. 7). Not only does the receptive field shift become larger with an attentional inhibitory surround, but the receptive field also appears to shrink around the position that now elicits the maximal response in the neuron, which is shifted towards the attentional locus (Fig. 7). This shrinking is seen to progressively increase as the attentional inhibitory surround becomes stronger (Fig. 7*B*). However, the RF shrinking occurs only when attention has an offset with respect to the neuronal preferred location. For attention focused right on top of the neuron's RF, one would see RF enlargement rather than



Figure 5. A recurrent network model with non-interacting attentional and sensory inputs can be in two different regimes regarding the receptive field shift induced by attention: shift away from attention (*A*) and shift towards attention (*B*). Upper panels show population activity profiles for stimuli at $x_S = 0$ in the unattended case (dashed line) and in the attended case (solid line and gray arrow, $x_A = 1$). Case A shows prominent attentional shift of the population activity profile whereas the dominant attentional modulation of the activity profile in case B is multiplicative scaling. In the lower panels of (*A*) and (*B*), the spatial tuning curve of the neuron at x = 0 is plotted versus stimulus positions in the unattended case (dashed line) and when attention is directed to the right side of the receptive field (solid line and gray arrow at $x_A = 1$). The two different regimes become clear as the maximum of the spatial tuning curve (inverted triangles) moves away from (*A*) or towards (*B*) the attentional focus. Responses and positions are in arbitrary units. (*C*) A recurrent network can be brought from away-from-attention shift to towards-attention shift by increasing the overall excitatory coupling. Results from a given simulation are plotted using the same shade of gray and symbol in each of the three panels. Attentional signal is always at $x_A = 1$. Spatial tuning curve (center panel) of the neuron in x = 0 for three simulations with identical parameters except for different strengths of recurrent connections (shown in left panel). The shift of the receptive field is quantified from the receptive shift indicates shift indicates shift indicates shift indicates shift away from attention. Parameters for (*A*) and (*B*) are given in the Materials and Methods section. In (*C*) the same parameters as in (*B*) were used except for J_0 , which is incrementally varied from -3 to 3.

shrinking (see Fig. 9). Notice that this effect does not require attentional inhibitory surround, but is a common feature of a strongly recurrent network, which we argue can be used to distinguish a recurrent from a feedforward architecture (see below).

In the regime of Fig. 5*A* where the receptive field shifts away from attention, we observed that the addition of an attentional surround inhibition increases the magnitude of the receptive field shift away from attention. On the other hand, the shrinking of the receptive field under inhibitory surround attentional input occurs also in this network regime (data not shown, but see Fig. 9).

RF Shifts Induced by an Adapting Stimulus

So far, we have focused on explaining the RF shift caused by attention (Connor *et al.*, 1996, 1997) by using two alternative computational architectures. Recently, however, there have been reports on shifts of neuronal tuning curves following protocols of visual adaptation in V1 (Dragoi *et al.*, 2000; Yao and Dan, 2001; Fu *et al.*, 2002; Felsen *et al.*, 2002) and in MT (Kohn and Movshon, 2004). A link between attention and adaptation is

suggested by the fact that adaptation is known to reduce the sensitivity to contrast, and attention has recently been shown to act as an effective increase in contrast (Reynolds et al., 2000; Martinez-Trujillo and Treue, 2002). Because of the potential interaction that such a relationship implies, we considered in our model how adaptation might shift the receptive fields of V4 neurons. The effect of a prior, long-lasting presentation of an adapting stimulus to our model neurons can be modeled as a reduction of excitability in a subset of neurons in our network during the course of our receptive field mapping procedure. The underlying, plausible assumption is that the time course of adaptation is much slower than the dynamics of receptive field changes that we are studying. Therefore, if an adapting stimulus is presented at location x_A for a long time and it induces visual adaptation, subsequent presentation of a test stimulus at location x will result in a network response to the test stimulus as if the network was receiving a constant hyperpolarizing bias current peaked at location x_A . We implement this by injecting a biasing hyperpolarizing input to the network (Carandini and Ferster, 1997; Sanchez-Vives and McCormick, 2000; Wang et al., 2003).

Our level of modeling is not explicit enough so as to identify a synaptic or intrinsic neuronal mechanism for this



Figure 6. A recurrent network can reproduce the results of Connor *et al.* (1997). Same simulation as in Figure 5*B*, except for attention being directed well outside the receptive field $\langle x_A = -2, +2 \rangle$. The dotted circle in the center of the figure represents schematically the measured receptive field size. Five equally separated stimuli are symmetrically positioned on the receptive field (central black bars numbered 1–5). Each of the three peripheral histograms shows the activity of the neuron to each of these five positions when attention is being directed to the smaller solid circle indicated by the arrow (upper histogram obtained for no attentional signal). (*A*) All five test stimuli are contained within the neuron's receptive field. A shift towards attention is observed. (*B*) The lateral test stimuli fall outside the receptive field. Responses are in arbitrary units. Compare with figure 2 of Connor *et al.* (1997).

adaptation: both mechanisms effectively reduce the excitability of neurons and would be modeled in the same way here. A scenario where adaptation occurs upstream from the modeled cortical circuit is also consistent with this implementation. Specifically, in our recurrent network model we use the same mathematical framework presented in Figure 2A but taking $\sigma_A =$ 0.71, $A_0 = 0$ and $A_1 < 0$. The broader extent of adapting, relative to attentional, additive input footprints (σ_A) is justified by the fact that the adaptation bias current is triggered by neuronal activity and therefore is comparable to the receptive field size, whereas the attentional beam can be more focused. For the simulation of adaptation-induced modulations in the feedforward scenario (Fig. 2B), we modeled the adaptation effect at the level of neural responses in the first layer, consistent with the finding of Kohn and Movshon (2004): we modify the equation for the first network to read: $R(y_j) = [I_S(x_i) + I_A(y_j) - T]_+$, and we use $A_0 = 0$, $A_1 = -0.2$.

The simulations show that in the two cortical networks that we consider here (Fig. 2), adaptation induces RF shifts in the opposite direction than attention (Fig. 9). We illustrate this explicitly for the recurrent network model (Fig. 2*A*) in Figure 8: adaptation gives rise to shifts of receptive fields towards or away from the adapted location, depending on whether recurrent connections are predominantly inhibitory or strongly excitatory, respectively (Fig. 8*C*).

Distinguishing the Models by their RF Modulations

We compared the different models quantitatively by examining how the receptive field of a neuron changes shape as an attentional spotlight is progressively moved away from the center of the RF (Fig. 9). We observe that neither of the three models (strong recurrent inhibition, strong recurrent excitation or feedforward) can be distinguished by means of the change in the neuron's maximal rate under attention (or adaptation). As is clear in Figure 9A, in all three cases, the presence of an inhibitory surround around the central focus of attention (dashed lines) is manifested by a firing rate reduction when attention comes to the flanks of the receptive field, and a firing rate increase for attention near the preferred location (as illustrated in Fig. 7B, left panel, when increasing the inhibitory surround, the focal excitation is compensatorily increased as well). Figure 9B shows the RF shifts for the three models. In contrast to the other two models, in a strongly inhibitory recurrent network attention induces away-from-attention shifts and adaptation induces towards-adaptation shifts, albeit small (compare shaded areas). In all three models, inhibitory attentional surround also manifests itself through a reversal of the sense of the receptive field shift when the location of attention focus is larger than a critical value. Note, again, that when the attention focus is beyond the RF boundary, RF shift is significant only in a recurrent network but not in a feedforward network.

Figure 9C displays the width of the receptive field (defined at half height). Interestingly, when attention is directed to the center of the RF (x = 0), both recurrent network models yield a larger RF width with attention than without it (left and middle panels, shaded areas). By contrast, the feedforward model predicts a narrower receptive field in the attended than in the unattended case (right panel, shaded area, see also Fig. 3B). The effect is also evident with adaptation: it narrows RF in recurrent models, whereas the opposite occurs in the feedforward model. Intuitively, one can understand this difference in the light of the different ways in which the attention/adaptation signals interact with the stimulus. In recurrent models, the modulatory signal is added together with the stronger sensory signal. When stimuli are varied in order to compute the tuning curve of a neuron, the modulatory signal received by this neuron is fixed. Because of this extra excitatory input, it is not surprising that the neuron's response to each stimulus is larger, hence the tuning curve (measured at half-height) is wider. The situation is different in the feedforward model. The output of a neuron y_i (in the first-layer) subject to an attentional bias input centered on y_A in the first layer is $R(y_j) = f_A(x_A - y_j)[I_S(y_j) - T]_+$, where $f_A(x_A - y_i)$ is a Gaussian function of the distance between the attention focus x_A and y_i . A neuron x_i in the second layer receives the weighted input $J(x_i - y_i)R(y_i)$. When the attention focus is near the center of its RF, $x_A \approx x_i$. Therefore, we can rewrite $J(x_i - y_j)R(y_j)$ as $J_{eff}(x_i - y_j)[I_s(y_i) - T]_+$, with $J_{eff}(y_j - x_i) = J(x_i - y_j)f_A(x_i - y_j)$. Because the product of two Gaussian functions is still a Gaussian with a narrower width σ_{eff} , given by $1/\sigma_{eff}^2 = 1/\sigma_I^2 + 1/\sigma_A^2$, attention modulation increases and sharpens the feedforward connectivity and results in a narrower receptive field of the neuron (notice that we define the width of a tuning curve or connectivity profile at half height, see Fig. 3B).

This result suggests that accurate measurements of the receptive field width with and without attention at the RF center may provide a test to differentiate between the recurrent



Figure 7. Receptive field shift can be large and its width can shrink significantly if the attentional signal mediates inhibition. (*A*) Simulation with surround inhibition shows significant receptive field shrinkage as a result of attentional input (lower panel, shrinking factor 0.9). The upper panel shows population activity profiles for stimuli at $x_S = 0$, while in the lower panel the spatial tuning curves of the neuron at x = 0 are plotted versus stimulus positions. Dashed lines correspond to the unattended case and for solid lines attention is directed to one side of the receptive field (solid line and gray arrow at $x_A = 1$). (*B*) Spatial tuning curves (center panel) of the neuron in x = 0 for three simulations with identical parameters except for varying attentional inputs (left panel). Right panel: shrinking factor (ratio of attended versus unattended RF sizes; see Materials and Methods) versus surround attentional input (value of attentional input at the location marked by the vertical arrow in the left panel). A shrinking factor below 1 indicates that attention induces the shrinking of the receptive field with respect to the unattended spatial tuning curve (black dashed line). Results from each simulation are plotted using the same shade of gray and symbol in all three panels. The parameters of Figure 5*B* are used but the details of the attention focus are modified: $\sigma_A = 0.53$, $\sigma_A' = 1.32$, A_0 is gradually decreased from $A_0 = 0.044$ to $A_0 = -0.23$ while A_1 always follows $A_1 = 0.085 - 1.82 A_0$. The example in (*A*) corresponds to $A_0 = -0.23$, and $A_1 = 0.5$.

and the feedforward scenarios. Note that there are two separate issues: whether attentional effects observed in the recorded area are primarily due to attentional input coming into this area or upstream from it, and whether recurrent circuitry in the recorded area has a substantial role in determining the attentional modulation of the shape of the RF. The test that we propose would rather address the latter issue, since a situation where attentional input targets upstream neurons and strong recurrent connectivity shapes RFs in the recorded area would yield similar results to our strong recurrent scenario.

Discussion

In recent years, electrophysiological studies of behaving primates have revealed the cellular correlate of selective visual attention at the single neuron level. In response to a single stimulus, multiplicative enhancement and receptive field shift towards attention were reported and interpreted as evidence for an attentional 'spotlight'. In addition, several lines of evidence have linked attentional effects to an increase in effective stimulus contrast. Since adaptation is known to induce a decrease of contrast sensitivity, this finding suggests an through the feedforward propagation of activity across visual areas or else through the interplay between an attentional 'spotlight' additive input and intrinsic local interactions within the cortical network (for example V4 or MT). Our main findings are: (i) the receptive field shift towards attention is not a direct consequence of a bias 'spotlight' model of attention; to understand this a clear distinction must be made between the activity of the neuronal network in response to a fixed stimulus and the single neuron's spatial tuning curve which defines its receptive field. (ii) Multiplicative enhancement by attention, either locally or upstream from the observed area, can give rise to receptive field shifts. In the local circuit model, both gain modulation and RF shifts may have a common underlying mechanism in intrinsic recurrent network connections. (iii) In the two-layer feedforward model without recurrent interactions, the range of RF shift induced in the second layer is limited by the strength and spatial extent of the attentional focus in the first layer, thus it does not seem to provide a plausible explanation for the shift effect of Connor et al. (1996, 1997). (iv) Receptive field shift can be accentuated by an attentional

interaction betwen attention and adaptation. In this paper, we

have studied how receptive field modulations can be induced



Figure 8. In the recurrent network model, adaptation to a long-lasting stimulus induces differential shifts in the receptive field depending on the regime of the intracortical connectivity. Tuning curve shifts (albeit small) towards the adapting stimulus when there is strong intracortical inhibition (*A*) and tuning curve shift away from adaptation when local excitatory feedback dominates the recurrence (*B*). (*A*) and (*B*) are analogous to their correspondents in Figure 5, but now the modulatory bias input is inhibitory rather than excitatory, thus simulating the effect of a previous adapting stimulus. (*C*) A recurrent network can be brought from weak towards-adaptation shift to away-from-adaptation shift by increasing the overall excitatory coupling. Results from a given simulation are plotted using the same shade of gray and symbol in each of the three panels. Adaptation focus always at $x_A = 1$. Spatial tuning curve (center panel) of the neuron in x = 0 for three simulations with identical parameters except for different recurrent connectivities (shown in left panel). Right panel: RF shift versus average connection strength. A positive shift indicates shift towards adaptation input. (*C*) Spatial tuning curves (center panel) of the neuron in x = 0 for three simulations are plotted using the same shade of gray and symbol in each of the three panels. (*D*) Spatial tuning curves (center panel) of the neuron in x = 0 for three simulations with identical parameters except for different recurrent connectivities (shown in left panel). Right panel: RF shift versus average connection strength. A positive shift indicates shift towards adaptation inputs (left panel). Right panel: Shift of the receptive field versus strength of adaptation input. Results from each simulation are plotted using the same shade of gray and symbol in all three panels. (Parameters in *A*, *B* and *C* are as in the corresponding panels of Fig. 5 except for $\sigma_A = 1$ and A_1 , which takes values -0.29, -0.07 and -0.07, respect

'spotlight' signal which includes surround inhibition to neurons in the periphery of the attentional focus. (v) Adapting stimuli on the flank of a neuron's receptive field also induce receptive field shifts, opposing those effected by attention.

Our results suggest that a detailed analysis of RF modulation by attention and adaptation will help to distinguish the prevalence of a recurrent versus a feedforward mechanism for the observed RF shifts. Specific predictions are: (i) adaptation protocols and attention tasks should produce opposite direction shifts when studied in the same cortical area and along the same stimulus dimension; (ii) towards-attention and awayfrom-adaptation shifts favor two alternative 'spotlight' scenarios: feedforward multi-layered, or strong excitatory recurrent networks. They differ in the RF size modulation when attention is directed right on the neuron's RF center: the feedforward architecture predicts a narrowing of the RF, whereas the recurrent network is associated with a broadening of the RF. This difference can be experimentally exploited to distinguish a recurrent from a feedforward scenario for RF shifts; and (iii) away-from-attention and towards-adaptation RF shifts can be accounted for, among the models considered here, by a strongly inhibitory coupled recurrent network. This regime may account for the experimental observations from MT neurons during visual adaptation (Kohn and Movshon, 2004).

Alternative Mechanisms for RF Shifts

So far, the mechanisms for receptive field attentional shifts proposed in the literature included dynamic modulations of



Figure 9. Comparison between three scenarios for the receptive field modulation induced by attention and adaptation. Results for recurrent network models are shown in the left and middle columns, corresponding to the strong inhibitory versus strong excitatory connections of Figure 5, respectively. The right column exhibits results from the two-layer feedforward model, where both adaptation and attention effects are applied in the first layer and propagated to the second layer via feedforward connections. The graphs show how receptive fields/tuning curves change their shape as a function of the distance between the modulatory input and the neuron's RF center (x = 0) in units of the unattended RF radius. (*A*) Peak firing rate relative to the non-attended/non-adapted case, (*B*) RF shift (positive values indicate shift in the direction of the focus of the modulatory input) and (*C*) RF width (defined at half-height) relative to the non-attended/non-adapted curve: inhibitory modulatory input (adaptation). Shaded areas indicate aspects that can help discriminate the various models, in (*C*) they cover the RF while in (*B*) they cover the area right beyond the RF boundary. For the recurrent networks, parameters are as in Figures 5 and 8 for attention and adaptation, respectively, whereas in the attention + surround case, the modulatory input parameters were $A_0 = -0.29$ and $A_1 = 0.81$ in the strongly inhibitory recurrent case, and $A_0 = -0.093$ and $A_1 = 0.25$ in the network with strongly excitatory connectivity (same as Fig. 7*B*, middle case). For the feedforward architecture, parameters are as in Figure 3.

synaptic strengths of intracortical connections (Olshausen *et al.*, 1993), and propagation of response gain changes in neurons of early visual areas to downstream networks (McAdams and Maunsell, 1999; Maunsell and McAdams, 2001). In this paper we present a third mechanism: strong recurrent connections among neurons in the local network.

Olshausen *et al.* (1993) propose that a network of control neurons exists, that operates on feedforward intracortical connectivity by changing synaptic weights in such a way that only information from a subregion of the scene is selectively routed to higher processing areas. In this scenario, the shift in the receptive field is an essential attentional modulation that creates position-invariant representations of stimuli. The partial shifts in area V4 would then be one step in the progressive shifting of receptive fields that would contribute to object-centered representations in higher-order brain areas. This scenario requires independent signals sent to each synapse of the visual processing feedforward network. However, a biophysically plausible mechanism for delivering such signals in real neural circuits remains elusive.

According to the feedforward model (McAdams and Maunsell, 1999; Maunsell and McAdams, 2001), attentional multiplication of responses would occur at a stage in the visual processing stream where receptive field size is congruent with the spatial attentional focus. The simple feedforward propagation of these attentional effects to a subsequent stage in visual processing induces shifts in the receptive fields of neurons in these downstream networks. Receptive field shifts in this framework are simply the reflection of upstream attentional gain modulation. We have shown here that this feedforward model cannot account quantitatively for the data of Connor et al. (1996, 1997) unless the attentional signal affects many neurons whose RFs do not overlap with the attentional focus. In addition, a prediction from this model is that strong attentional response gain control (>50% increase) should occur earlier in the visual pathway than response shifts induced by attention. Experimental evidence consistent with this idea comes from imaging experiments on humans, that show attentional modulation as far down as the thalamus (O'Connor et al., 2002; Kastner et al., 2003) and primary visual cortex (Tootell et al., 1998; Ito and Gilbert, 1999; Gandhi et al., 1999; Somers et al., 1999; Brefczynski and DeYoe, 1999). In contrast, electrophysiological experiments in the monkey have usually found little attentional gain field modulation in the primary visual cortex, and weak to moderate effect in V2 (Motter, 1993; Luck et al., 1997; McAdams and Maunsell, 1999; Marcus and Van Essen, 2002; but see Roelfsema et al., 1998; Vidyasagar, 1998). On the other hand, the idea that the attentional 'spotlight' input is directed onto a brain area whose

typical RF size is commensurate with the attentional focus is challenged by recent fMRI evidence (Müller *et al.*, 2003). Also, the grain of visual spatial attention has been estimated to be \sim 3 times coarser at the fovea than visual resolution and significantly coarser than the spatial resolution of cells in V1, at least for certain tasks (He *et al.*, 1996; Intriligator and Cavanagh, 2001). This is in line with the idea that the attention signal is much wider than RF size in V1.

In this paper we have presented an alternative mechanism, where each module in the processing hierarchy generates its attentional effects (multiplication and shift) through recurrent interactions between neurons in the local circuit (Salinas and Abbott, 1996). Here, attentional modulation does not need to target only the brain area whose receptive field size matches the required extent of the spatial spotlight, but both multiplicative and shift effects will be induced locally by the internal circuitry of each brain area. We emphasize that these scenarios are not mutually exclusive, they could interact in some areas, or they could differentially control the attentional effects in different brain areas or for different stimuli feature dimensions.

The fact that our argument favors the recurrent network versus the feedforward network scenario on the basis of the phenomenology when attention is focused outside the neuron's RF, might raise some concerns regarding how well defined the RF borders can be in the experiment. Indeed, RF borders might have been underestimated in Connor *et al.* (1996, 1997) so that attention was actually being focused within the neuron's RF and then our feedforward model could still be in agreement with the data. However, this is unlikely to be the case because our measure of receptive field size –width at half height– is much more conservative than that in (Connor *et al.*, 1997).

Network Activity Profile versus Single Neuron Tuning Curve

We have shown that single unit electrophysiological measurements of receptive fields during spatial attention tasks may have qualitatively very different properties than the single-trial network population activity. We have shown this heuristically in Figure 1 and in a recurrent network model. In Figure 5, even though population activities always shifted toward the attentional focus, the spatial tuning curve in one case shifted away (Fig. 5*A*) and in the other case towards attention (Fig. 5*B*).

Without attentional signal, a single cell's RF and a population activity profile have the same shape. This stems from the fact that it is symmetrical to either look at one cell while varying the stimulus (RF), or consider different cells across the entire population for a given stimulus (network activity). Such a symmetry no longer holds in the presence of a fixed attention bias, because the distance between the stimulus and the focus of attention is fixed when different cells are considered to compute a population activity pattern, whereas this distance is obviously not constant when the stimulus is varied to compute a single cell's tuning curve. A way to circumvent this and have access to the population activity profile in single-neuron experiments is to change the attentional location together with the stimulus when plotting a neuronal response curve, so that the relative distance between their locations remains constant (see Martinez-Trujillo and Treue, 2004). This situation implies that caution must be exercised in interpreting the data, since it cannot be assumed in general that receptive fields are experimental probes of population activity profiles. Also, the

perception and behavioral choices of the animal are based on the single-trial network activity, rather than the single-neuron responses to a variety of different stimulation conditions. Therefore, theories of attention based on these electrophysiological experiments need to carefully assess what single-neuron responses say about the network function.

Receptive Field Shifts

We showed that, if attentional modulation acts on a strongly recurrent network, the receptive field shift towards attention (Connor et al., 1996, 1997) can occur as an automatic consequence of attentional multiplicative scaling of responses, rather than a result of a simple enhancement of firing around the attentional focus (directly by a 'spotlight' bias input). To obtain the observed receptive field shift, we claim that attention needs to induce a multiplicative scaling of the population activity profile (Fig. 1C). One way for this to happen in a recurrent model network, is to have it operate in the regime described by Salinas and Abbott (1996). Briefly, cortical amplification through localized recurrent excitatory feedback has a greater effect on active neurons (peak of the bump) than inactive neurons (tails of the bump). This translates in an approximate multiplicative scaling of responses upon the addition of a fixed constant current to all neurons in the network. Thus, toward-attention RF shifts can be accomplished in recurrent networks for sufficiently strong local excitatory recurrent interactions, as illustrated in Figure 5C.

Interestingly, our model shows that, even if the spatial range of attention is much smaller than the typical receptive field size in that area, recurrent interactions within a local network can by themselves produce the observed receptive field shifts. Thus, the attentional signal might not need to be exclusively gated to the area matching the size of the attentional 'spotlight' and that of the receptive field. It remains to be explored what is the combined effect of attentional signals in several (possibly reciprocally connected) layers of recurrent neural networks of the kind that we explored in this paper.

Partial receptive field shifts have also been observed in the context of multimodal integration, and are usually attributed to the convergence of inputs in distinct frames of reference (Deneve *et al.*, 2001; Pouget *et al.*, 2002; Xing and Andersen, 2000). Thus, over a wide spectrum of behavioral contexts RF shifts may represent fundamental computational operations in the cortex, and they might operate through distinct physiological mechanisms.

Attention-gated Surround Inbibition

In our recurrent single network model, the largest shift in the receptive field is obtained when the attentional signal contains an inhibitory component around the attentional locus. The action of attention through focal excitation and surround inhibition has been put forward before (Treisman, 1988; Crick and Koch, 1990; Tsotsos, 1990; Tsotsos *et al.*, 1995; Cutzu and Tsotsos, 2003). Here we report another functional implication of such an attentional signal, in the context of receptive field shifts.

Such a scheme is consistent with some recent anatomical and physiological data showing the involvement of disynaptic inhibition in feedback 'top-down' projections to early visual cortex. In anesthetized animals, there is functional evidence of inhibitory interareal feedback interactions (Alonso *et al.*, 1993; Martínez-Conde *et al.*, 1999), which in many cases is only unmasked when stimuli span across the surround area of the receptive field (Hupé et al., 1998; Bullier et al., 1996; Wang et al., 2000). We emphasize that an attentional surround inhibition is not likely to arise from direct 'top-down' projections; indeed long-distance interareal synaptic connections could be exclusively excitatory. But attentional surround inhibition could be realized by 'top-down' excitatory inputs to inhibitory neurons in the early sensory areas, which in turn send lateral inhibition to pyramidal neurons. Anatomically, there is evidence that inhibitory neurons are indeed targets of feedback corticocortical axons in visual cortex (Gonchar and Burkhalter, 1999; Johnson and Burkhalter, 1996; Gonchar and Burkhalter, 2003; but see Shao and Burkhalter, 1996). Taken together with the existence of spatially extended projections from interneurons onto pyramidal cells (Crook et al., 1998), this provides a possible anatomical substrate for surround inhibition mediated by corticocortical feedback projections.

RF Shifts Induced by Adaptation and Attention

Partial shifts in the selectivity of neurons are not restricted to area V4 and are not a unique attentional footprint: just prior to a saccadic eve movement, LIP (Duhamel et al., 1992) and V4 (Tolias et al., 2001) neuronal receptive fields shift towards the planned target. This has strengthened the idea that saccadic eye movements and shifts of attention are closely linked. On the other hand, orientation tuning curves of V1 neurons change their preferred orientation as the result of adaptation to a previous oriented stimulus (Müller et al., 1999; Dragoi et al., 2000; Felsen et al., 2002). In all these studies, the shift of the tuning curves is away from the adapted orientation. In contrast, motion direction tuning curves in area MT have been reported to shift towards an adapting stimulus (Kohn and Movshon, 2004); according to our model, this observation would be compatible with a recurrent inhibitory architecture in MT. In addition, when the adapting stimulus is more complex and includes the repetition of a temporal sequence, Yao and Dan (2001) and Fu et al. (2002) have shown that orientation tuning curves and receptive fields shift in a direction which is dependent on the relative ordering of the repeating sequence, suggesting the involvement of a spike-timing-dependent plasticity mechanism. A possible mechanistic scenario that has been explored in a computational model is when adaptation induces short-term plasticity in the recurrent intracortical connections engaged by the adapting stimulus (Teich and Qian, 2003; Felsen et al., 2002).

Thus, shifts in neuronal selectivity are widespread in the visual system and could underlie perceptual effects related to selective attention and adaptation. So far, there are no physiological studies in which both attention and adaptation have been examined for their effect on a single visual feature selectivity (such as spatial position, orientation, velocity), and in the same visual area. The prediction from our study is that if an area shows both attentional and adaptation electrophysiological effects in the selectivity of neurons, they should oppose each other and a detailed analysis of their interrelationship (Fig. 9) could shed light onto the relative importance of the feedforward versus recurrent architecture for the generation of tuning curve modulations induced by attention and adaptation.

Why Receptive Field Shifts?

We have focused here on the interpretation and mechanisms for neuronal receptive field shifts induced by attention and adaptation, as observed electrophysiologically. We have shown that these shifts can be informative to reveal the underlying architecture responsible for attentional modulations, and we have also shown that they can be misleading. Indeed, shifts in receptive fields (or for that matter, any tuning curve shift) do not necessarily reflect an underlying population activity shift in the same direction. However, the real purpose of attentional mechanisms in the brain is to implement behaviorally advantageous modulations in the brain activity in a single trial, rather than neuronal tuning curves that are meaningful only across trials. Therefore, if selectivity shifts have any relevance for attentional (or adaptation) control, it must be in the context of what shifts are induced in population activity profiles. So far, experiments have looked at single neurons, but a more direct survey of population activity via multiple simultaneous recordings or optical imaging might be necessary in order to understand the dynamics of cortical activity induced by focal selective attention.

One possibility is that selectivity shifts emerge as a byproduct of response gain changes. Note however that it has been argued that intrinsic recurrence involved in gain changes cannot increase the information content of the signal (Pouget et al., 2000), although they do modify the sensory representation and thus their processing in downstream areas. Alternatively, population activity shifts, other than being an epiphenomenon of response gain modulations, may be a fundamental mechanism for selective information processing. For instance, shifts in the network population activity by covert attention could enhance spatial resolution (Yeshurun and Carrasco, 1998), and attentional control over visual resolution could serve the cognitive process of object recognition (Deco and Schürmann, 2000). As far as we know, no one has assessed in detail how an attentional biasing signal resulting both in gain modulation and activity shift changes the input-output information transfer in a sensory area, or the functional impact of the sensory representation in downstream information processing. These are interesting issues worth analyzing in future research.

Notes

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Appendix

We present here analytical calculations for the feedforward model. A neuron in the second network whose preferred selectivity is at *x* fires at rate $R(x,x_S,x_A)$ when a stimulus is presented at location x_S and the attention signal is focused on x_A :

$$R(x, x_{s}, x_{A}) = \int dx' (1 + A_{1} e^{-0.5(x' - x_{A})^{2}/\sigma_{A}^{2}})$$

$$S_{1} e^{-0.5(x' - x_{S})^{2}/\sigma_{S}^{2}} J_{1} e^{-0.5(x' - x)^{2}/\sigma_{J}^{2}}$$
(1)



Figure A1. Tuning curve shift in the feedforward model is limited when attention is allocated beyond the receptive field boundaries of second-layer neurons. It is necessary to have both very strong attentional modulation in the first network and not very dissimilar tuning curve widths in both layers (*C*). Alternatively, attentional modulation of first-layer neurons must have a very broad footprint, approaching the size of second-layer neurons' RFs (*D*). (*A*) Absolute tuning curve shift x_S versus location of attention in units of the second-layer RF size Δ_0 : x_A/Δ_0 . Analytical calculations (solid line, see Appendix) replicate simulations (shaded area). Same parameters as Figure 9*B* right, solid line: $\sigma_S = \sigma_A = 0.21$, $\sigma_A/\sigma_J = 0.3$, $A_1 = 0.5$. (*B*) relative shift $x_r = x_S/x_A$ versus relative location of attention in units of the second-layer RF size $\chi = \Delta_A/\Delta_0$, beyond which focused attention is unable to induce tuning curve shifts. In the example shown in this panel $\chi = 0.81$. (*C*) χ plotted against the strength A_1 of firing rate modulation by attention. This is shown for two ratios of unattended RF sizes in first- and second-layer neurons. Here attention has the same footprint as first-layer neurons' RFs. Notice that the dynamic range χ can only be beyond receptive field boundaries ($\chi > 1$) if attentional modulation is unreasonably strong ($A_1 \sim 1$ in solid line) or if the receptive fields of second- and first-layer neurons' RFs. If the footprint of the attentional foccus to second-layer neurons' RFs. If the footprint of the attentional focus is larger than the first-layer neurons' RFs, it is possible to obtain $\chi > 1$ albeit for smaller yet biologically plausible, relative shifts x_0 . Filled circle indicate points corresponding to (*A*) and (*B*). (*D*) χ (Left panel) and x_0 (Right panel) versus relative size of attentional focus to second-layer neurons' RFs. If the footprint of the attentional focus is larger than the first-layer neurons' RFs, its possible to obt

Simple algebraic manipulations allow one to derive the tuning curve width (half-width at half height) of neurons in the second network in the absence of attentional signal $(A_1 = 0)$:

$$\Delta_0 = \sigma_s \sqrt{2 \ln 2 \left(1 + \frac{\sigma_f^2}{\sigma_s^2}\right)}$$
(2)

We focus on one arbitrary neuron in the second network without loss of generality (x = 0). Without attention the firing response is maximum when $x_s = 0$. In order to study the tuning curve shift induced by the attentional signal fixed at x_{4} , we look for the stimulus location x_s at which the firing rate $R(0, x_s, x_A)$ is maximum. By setting to zero the derivative of expression (1) with respect to x_s the shift in the tuning curve relative to the position of attention, $x = x_s/x_{A_b}$ is obtained as the solution of the implicit equation: x = f(x), where

$$f(x) = A_1 \left(\frac{y^2 + z^2}{1 + y^2 + z^2}\right)^{3/2} \frac{1 - (1 + z^2)x}{z^2}$$
$$\exp\left\{-\frac{1}{2} \frac{x_A^2}{\sigma_A^2} \left[1 - \frac{(1 + y^2 x)^2}{1 + y^2 + z^2} + \frac{y^4 x^2}{y^2 + z^2}\right]\right\}$$
(3)

with $y = \sigma_A / \sigma_S$ and $z = \sigma_A / \sigma_F$ Solving this implicit equation numerically for different values of x_A , and using the parameters of Figure 9 produces a curve that overlaps the continuous trace in panel B of Figure 9, for the feedforward model. This is explicitly shown in Figure A1A, where the shaded area is as in the simulation and the overlapping curve is the solution of the equations.

It is easy to obtain from the equations the initial slope of this curve (we name it x_0) by setting $x_A = 0$ in equation (3) and then solving x = f(x) (see Fig. A1*B*). The value of x_0 indicates the magnitude of the fractional shift when x_A approaches 0: for $x_0 = 1$ the RF shifts all the way from the preferred value to the attention location, whereas for $x_0 = 0$ the RF does not shift at all. The mathematical expression for x_0 is:

$$x_0 = \frac{1}{1 + z^2 + \frac{1}{A_1} z^2 \left(\frac{1 + y^2 + z^2}{y^2 + z^2}\right)^{3/2}}$$
(4)

We can now define the dynamic range of the attentional shift Δ_A as the value of x_A along the network at which the relative RF shift *x* decays to one-half of x_0 (see Fig. A1*B*). This gives a measure of the distance from the receptive field center beyond which tuning curve partial shifts (of whatever magnitude) cease to happen. One obtains:

$$\Delta_{A} = \sigma_{A} \sqrt{\frac{2}{1 - \frac{(1+y^{2} x_{D}/2)^{2}}{1+y^{2}+z^{2}} + \frac{y^{4}(x_{D}/2)^{2}}{y^{2}+z^{2}}} \ln \left[2 + A_{1} \frac{1+z^{2}}{z^{2}} \left(\frac{y^{2}+z^{2}}{1+y^{2}+z^{2}}\right)^{3/2}\right]}$$
(5)

To get an idea of how far the attention focus can be from the RF center, still inducing RF shifts in the second-layer neurons, we plot in Figure A1 *C* $\chi = \Delta_A / \Delta_0$ versus the attentional modulation strength A_1 for two different situations: first-layer RF size smaller than second-layer RF size (solid line) and approximately same RF sizes in both layers (dashed line). Note that the ratio of first- to second-layer RF sizes is given by $1/\sqrt{1+(y/z)^2}$. To plot these curves we make use of equations (2) and (5). Thus, $\chi = 1$ implies that receptive field shifts can be obtained up until attention is focused right on the very edge of the receptive field; instead $\chi < 1$ means that no attentional shift can be induced when attention is on or beyond the receptive field boundary. The assumption in the feedforward model proposed in the literature (McAdams and Maunsell, 1999; Maunsell and McAdams, 2001) is $\sigma_A = \sigma_S$ (i.e. $\gamma = 1$): the attentional focus targets a cortical area where the receptive field size is congruent with the attentional focus. Note that in this situation $\boldsymbol{\chi}$ depends only on the ratio of first-layer to second-layer footprints $z = \sigma_A / \sigma_I$ and on the strength of the multiplicative attentional modulation in the first layer A_1 . The constraints of this model are illustrated in Figure A1C, showing that, if attention is being directed outside of the neuron's receptive field, receptive field shifts can only be induced for unreasonably strong attentional modulation (so that, for example, the firing rate is doubled when $A_1 = 1$. Experiments typically see modest rate increases electrophysiologically, ~10%), or for networks with very similar RF sizes (also in contradiction with the hierarchical properties of visual areas). A more flexible feedforward structure, however, can reproduce the experimental phenomenology if attentional modulation on the firstlayer network is allowed to affect a larger subpopulation of neurons $(\sigma_A > \sigma_S)$ see Fig. A1D). Even in this situation, reaching the magnitude of RF-shift range of the recurrent model (Fig. A1E) requires very strong attentional modulations in the feedforward model (A1>2, i.e. >200% increase).

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