

Adaptation in the corticothalamic loop: computational prospects of tuning the senses

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The present article discusses computational hypotheses on corticothalamic feedback and modulation of cortical response properties. We have recently proposed that the two phenomena are related, hypothesizing that neuronal velocity preference in the visual cortex is altered by feedback to the lateral geniculate nucleus. We now contrast the common view that response adaptation to stimuli subserves a function of redundancy reduction with the idea that it may enhance cortical representation of objects. Our arguments lead to the concept that the corticothalamic loop is involved in reducing sensory input to behaviourally relevant aspects, a pre-attentive gating.

Keywords: corticothalamic loop; feedback; adaptation; velocity tuning; object segmentation; pre-attentive gating

1. COMPUTATIONAL VIEWS OF CORTICOTHALAMIC FEEDBACK

The thalamus is the major gate to the cortex for peripheral sensory signals, for input from various subcortical sources, and for re-entrant cortical information. Cortical information processing thus fundamentally depends on its thalamic input. Thalamic nuclei, in turn, perform some operation on the signals they relay while being modulated by various transmitter systems (McCormick 1992) and under the influence of massive feedback from their cortical target areas (Guillery 1995; Sherman 1996; Sherman & Guillery 1996). In view of the complexity of the thalamo-cortical network, one is compelled to believe that the thalamus not merely *delivers* information to the cortex but that cortical processing is somehow *entangled* with thalamic processing. Accordingly, it seems natural that cortical functioning cannot be properly understood without taking into account the corticothalamic feedback loop.

Whereas it is well established that the response characteristics of many neurons in primary sensory cortices are roughly shaped by different types of convergent thalamic inputs (Saul & Humphrey 1992*a,b*; Reid & Alonso 1995; Alonso *et al.* 1996; Ferster *et al.* 1996; Jagadeesh *et al.* 1997; Murthy *et al.* 1998; Hirsch *et al.* 1998), the modulation effected by cortical feedback in thalamic response has been difficult to interpret. Nonetheless, experiments and theoretical considerations have produced a variety of views of corticothalamic function. Most of these are concerned with the primary visual pathway—the LGN and the primary visual cortex.

(a) *Gating and enhancement of neural response*

The ideas put forward to date are conceptually mainly of two kinds. On the one hand one offers an open-loop understanding of corticogeniculate feedback, proposing an operation of the visual cortex on the LGN, while deferring its control to some other, more complex process not considered. Examples of such computational concepts are attention-related gating of GRCs (Sherman & Koch 1986), gain control of GRCs (Koch 1987; Rivadulla *et al.* 2002), increasing transmitted information in GRC output (McClurkin *et al.* 1994) and switching GRCs from a detection to an analysing mode (Godwin *et al.* 1996; Sherman 1996; Sherman & Guillery 1996). On the other hand one argues in favour of a positive or negative feedback signal for responses in the corticogeniculate loop. Its effect would be to amplify certain response characteristics such as length (Murphy & Sillito 1987; Rivadulla *et al.* 2002) and orientation tuning (Sillito *et al.* 1994; Singer 1994; Murphy *et al.* 1999). A positive feedback loop has also been proposed to underlie stabilization of learning in the geniculocortical pathways (Grunewald & Grossberg 1998).

With rather vague open-loop and simple feedback concepts of corticothalamic operation, it seems probable that today, after almost 30 years of studying the subject (Singer 1977), there is still a long way to go to arrive at an integrated view of thalamocortical functioning. We believe that computational modelling, although to some extent speculative, can play an important part in this endeavour, as it does in understanding brain function in general (Van Hemmen & Sejnowski 2003). Experimental data in neuroscience are interpreted functionally in the light of computational metaphors. It is thus crucial to continuously refine the repertoire of the metaphors we use. Computational modelling will lead to the development of more sophisticated functional concepts to be matched with empirical data.

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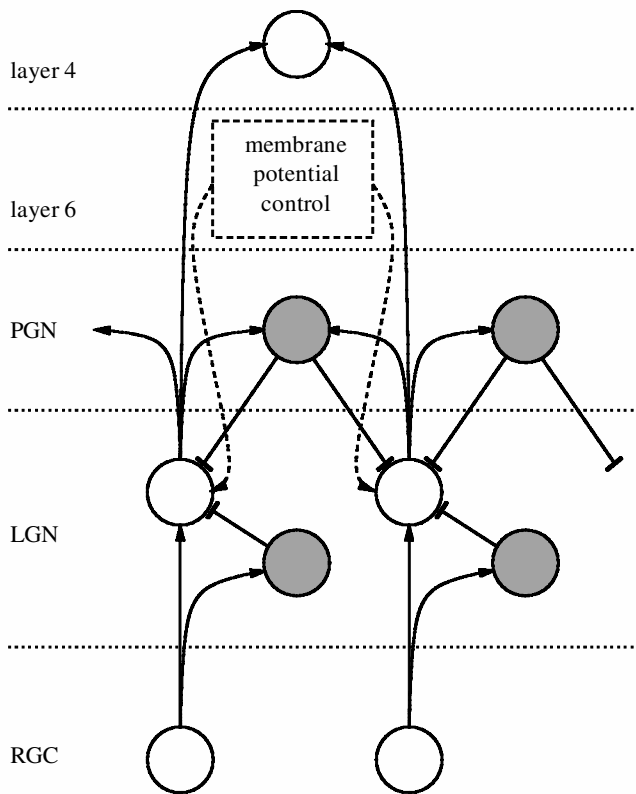


Figure 1. A network model of the primary visual X-pathway we have studied. The open circles and arrowheads indicate excitatory neurons and their respective synapses, and the grey circles and bars indicate inhibitory neurons and their respective synapses. A retinal X-ganglion cell (RGC) sends its axon to the LGN and synapses excitatorily on an X-relay cell (white circle) and on an intrageniculate interneuron (grey circle), which in turn inhibits the same relay cell. This synaptic circuit is called a 'synaptic triad'. There is an inhibitory feedback loop via the PGN. The relay cells' output converges in cortical layer 4, where it lays out the basic spatiotemporal structure of simple cells' RFs. The influence of cortical feedback, originating from cortical layer 6, has been modelled as a modulation of the relay cells' membrane potential. For the complete set of equations describing the model see the appendices in Hillenbrand (2001).

(b) *Tuning of neural-response preference*

As compared with corticogeniculate feedback, our understanding of RFs in the primary visual cortex is relatively advanced. It may thus be a revealing perspective to try to understand corticogeniculate feedback functionally in terms of its modulation effects on cortical RFs.

Recently, we have elaborated the idea that the visual cortex controls, via feedback, the temporal response properties of GRCs in a way that alters, in turn, the preference of cortical cells for stimulus speed (Hillenbrand & Van Hemmen 2000, 2001; Hillenbrand 2001). Figure 1 shows the model of the primary visual pathway we have studied. In brief, we have investigated a model of cat GRCs that comprises 12 ionic membrane conductances, giving rise to the typical thalamic patterns of activity such as tonic and burst components of responses (Huguenard & McCormick 1992; McCormick & Huguenard 1992). We have subjected these model neurons to direct excitatory and indirect inhibitory synaptic input (cf.

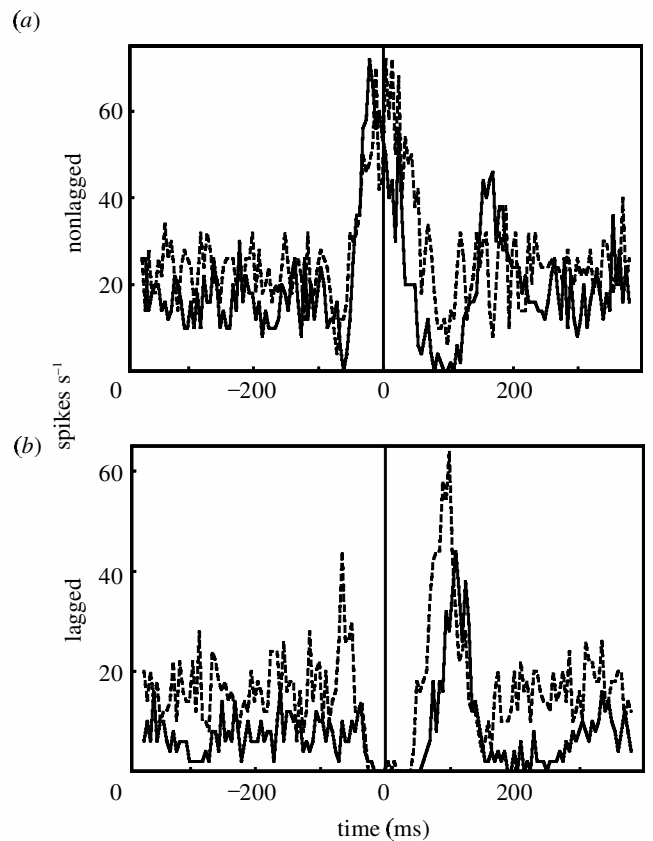


Figure 2. Computer simulation of a moving-bar response of a single relay neuron at the two resting membrane potentials of -72 mV (solid lines) and -61 mV (dashed lines). (a) Typical nonlagged responses are reproduced with strong feed-forward excitation and weak feed-forward inhibition and (b) typical lagged responses with weak feed-forward excitation and strong feed-forward inhibition; cf. figure 1. The time of the retinal input peak has been set to zero. It turns out that the nonlagged bar response peak shifts to earlier times as the membrane is hyperpolarized. Conversely, the lagged bar response shifts to later times. The rates are averaged over 100 bar sweeps. (Adapted from Hillenbrand & Van Hemmen (2001).)

figure 1) as recorded from the retina during visual stimulation. We have found that, just by varying the relative strengths of excitation and inhibition, the temporal response of GRCs splits into two distinct types: one resembling a nonlagged, the other a lagged response (Mastrorarde 1987; Humphrey & Weller 1988; Saul & Humphrey 1990); see figure 2 for some simulated responses. Moreover, the two response types react to changes in their membrane potential in an opposite manner. With hyperpolarization, the nonlagged-type neurons shift their peak response to a moving bar to earlier times, whereas the lagged-type neurons shift their peak response to later times; see figure 2. Numerous studies (Saul & Humphrey 1992*a,b*; DeAngelis *et al.* 1995; Jagadeesh *et al.* 1997; Murthy *et al.* 1998) indicate that GRCs of the two types converge, directly or indirectly, onto the same neurons in the primary visual cortex and lay out the basic spatiotemporal structure of simple cells' RFs. Consequently, the preference of cortical neurons for moving local features (bars, contrast edges, dots, etc.) is predicted

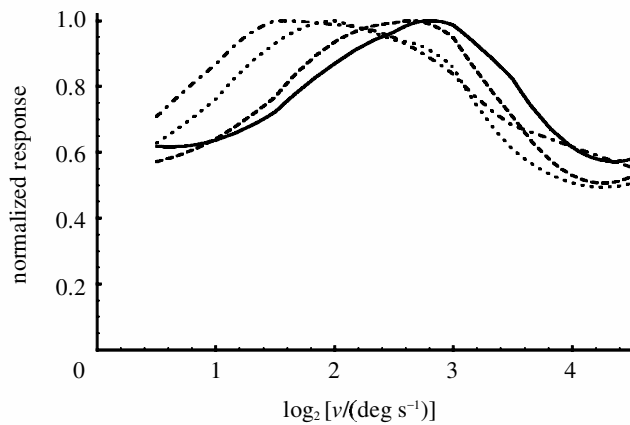


Figure 3. Computer simulation of the geniculate moving-bar response and input to visual cortex at various geniculate resting membrane potentials. We show second-order polynomial fits to the normalized mean response rate (30 bar sweeps) of the combined lagged and nonlagged neural populations as a function of the bar velocity v (logarithmic, base 2). It turns out that the total geniculate response peaks at progressively lower velocities as relay cells are hyperpolarized. Solid line, -61 mV; dashed line, -66.5 mV; dotted line, -72 mV; dot-dashed line, -76 mV. (Adapted from Hillenbrand (2001).)

to shift to *lower speeds* as GRCs are *hyperpolarized* and to *higher speeds* as GRCs are *depolarized*; see figure 3.

The effect of both feed-forward inhibition and resting membrane potential on GRCs' response timing is mediated largely by the low-threshold Ca^{2+} current I_T and its tendency to produce burst spikes after sufficient hyperpolarization (Huguenard & McCormick 1992; McCormick & Huguenard 1992). With only weak feed-forward inhibition, nonlagged neurons respond to retinal input with immediate depolarization, eventually reaching the activation threshold for the Ca^{2+} current. If the Ca^{2+} current is in the de-inactivated state, it will boost depolarization and give rise to an early burst component of the visual response. The lower the resting membrane potential, the more de-inactivated and, hence, stronger the Ca^{2+} current will be, and the stronger the early burst relative to the late tonic response component. Lagged neurons, however, receive strong feed-forward inhibition and, hence, initially respond to retinal input with hyperpolarization. Repolarization occurs when inhibition gets weaker. This may result either from cessation of retinal input or from adaptation, i.e. fatigue, of the inhibitory input to GRCs. With the Ca^{2+} current I_T being de-inactivated by the excursion of the membrane potential to low values, lagged spiking starts with burst spikes as soon as the voltage reaches the Ca^{2+} -activation threshold. This will take longer if the resting membrane potential is lower, leading to the shift in response timing with membrane polarization observed during the simulations.

Modulation of the GRCs' membrane potential by cortical feedback can result directly from the action of metabotropic glutamate and *N*-methyl-D-aspartate receptors, leading to depolarization (McCormick & Von Krosigk 1992; Godwin *et al.* 1996; Sherman 1996; Sherman & Guillery 1996; Von Krosigk *et al.* 1999), and indirectly, via the PGN or geniculate interneurons, from activation of GABA_B (γ -aminobutyric acid type B) receptors,

resulting in hyperpolarization of GRCs (Crunelli & Leresche 1991; Sherman & Guillery 1996; Von Krosigk *et al.* 1999). Moreover, GRCs may be indirectly depolarized by the action of group II metabotropic glutamate receptors on PGN neurons (Cox & Sherman 1999).

For the predicted effect of feedback on cortical velocity tuning no direct experimental evidence is available yet. Dynamic velocity preference, however, has indeed been recently observed in the visual cortex (Li *et al.* 1999; Phinney & Siegel 2000).

As a result of adaptive velocity preference, the cortex would be able to tune into certain parts of a dynamic stimulus. We have developed a functional hypothesis of *velocity-preference tuning* as a mechanism to detect and represent coherent, object-related motion from the nonlocal velocity distribution of a stimulus (Hillenbrand & Van Hemmen 2000; Hillenbrand 2001). In § 2 we will present this tuning idea in the context of others about adaptive changes of cortical representation.

2. COMPUTATIONAL VIEWS OF ADAPTIVE NEURAL RESPONSES

It is instructive to gain a somewhat broader perspective of adaptive cortical-response properties. To this end, we consider possible scenarios of adaptation to certain stimulus conditions. We then go on to discuss the example of velocity-preference tuning in a specific functional manner. In particular, we contrast our proposal of *coherence representation* with the popular view of *redundancy reduction* as a short-term adaptive process.

(a) *Four generic scenarios of response adaptation*

Perceptual repulsion is a phenomenon that is characteristically associated with adaptation to certain stimulus conditions. After having viewed a grating of a fixed orientation for an extended period of time (roughly a minute or longer), subsequently presented gratings of similar orientation are perceived as tilted away from the original, adapting orientation. This is the tilt after-effect (Gibson & Radner 1937; Blakemore & Campbell 1969; Campbell & Maffei 1971). A similar effect of perceptual repulsion is induced by presenting a grating together with a second one at a slightly oblique angle, known as the tilt illusion (Blakemore *et al.* 1970; Smith & Wenderoth 1999). Analogous repulsion is also known for size (Blakemore & Campbell 1969), stereoscopic depth (Stevenson *et al.* 1991) and velocity perception (Clymer 1973; Marshak & Sekuler 1979; Smith & Edgar 1994; Schrater & Simoncelli 1998). Perceptual repulsion, hence, seems to be a rather universal pattern of interaction between stimuli, in both space and time. When analysing adaptation of neural representation to stimulus conditions, it may thus be worthwhile to keep an eye on this effect.

We now consider four generic scenarios of changes of cortical representation in response to an adapting or inducing stimulus. We are interested in how they relate to perceptual repulsion. The scenarios are:

- (i) depression of responses of neurons preferring the adapting or inducing stimulus;
- (ii) facilitation of responses of neurons preferring the adapting or inducing stimulus;

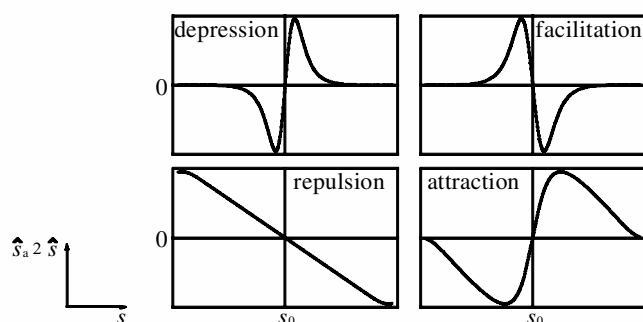


Figure 4. The four scenarios of response adaptation; see § 2a for details. For each scenario, the plot shows the difference $\hat{s}_a - \hat{s}$ between the perceived stimulus values for the adapted and unadapted neural populations as a function of the test-stimulus value s . The vertical line in each plot represents the adapting or inducing stimulus s_0 , the horizontal line indicates a perceptual difference of zero. Perceptual repulsion is seen to occur for the depression and attraction scenarios.

- (iii) repulsion of neural preferences from the adapting or inducing stimulus; and
- (iv) attraction of neural preferences towards the adapting or inducing stimulus.

Let s be the orientation of a grating, the speed of a moving stimulus, or some other stimulus property within an appropriate range. Furthermore, let r_i be the response rate of neuron i belonging to a population $1 \leq i \leq n$. The neuron's response is determined by its tuning characteristic $r_i = g(s - p_i)$, where g is taken to be a Gaussian function and p_i is the neuron's stimulus preference. The perceived stimulus \hat{s} is assumed to be recovered from a neural population code through

$$\hat{s}(s) = \frac{\sum_{i=1}^n r_i p_i}{\sum_{j=1}^n r_j} = \frac{\sum_{i=1}^n g(s - p_i) p_i}{\sum_{j=1}^n g(s - p_j)}, \quad (2.1)$$

the perceived value being the average of all neural preferences in the population, weighted by each neuron's response. In the case of a cyclic stimulus dimension such as orientation, s may be chosen to parameterize points on a unit circle. The qualitative results presented here, however, do not depend on this choice. Likewise, absolute values of s do not have any meaning and are thus omitted.

Let \hat{s} be the perceived value for an unadapted neural population, \hat{s}_a for an adapted one. In figure 4 we show plots of the perceptual difference $\hat{s}_a - \hat{s}$ as a function of the test stimulus s for the four adaptation scenarios described earlier. Evidently, response depression and attraction of neural preferences are both consistent with the phenomenon of perceptual repulsion whereas response facilitation and repulsion of neural preferences are not. Thus, it would seem that recent reports of repulsive shifts in neural preferences away from an adapting orientation (Dragoi *et al.* 2000, 2001) do not directly relate to the mechanism underlying the tilt after-effect. Likewise, reported shifts of neural preferences away from a moving inducer's speed (Li *et al.* 1999) do not contribute to, but rather diminish, perceptual velocity repulsion.

We note that there are a lot of free parameters in this

very simple model, e.g. the shape of tuning curves, the number of neurons in the population and the form of depression or of shifts in neural preferences. Moreover, although population coding is a common view of neural representation (Salinas & Abbott 1994; Lewis 1999), any particular form such as equation (2.1) is debatable. All these parameters can influence the shape of the perceptual curves in figure 4. Here, however, we are only interested in the qualitative perceptual effect, which does not depend critically on these parameters.

It may be worth mentioning that another perceptual phenomenon that accompanies repulsion is in fact dependent on it. Discrimination of orientation is known to be enhanced near the adapting orientation, impaired further away from it and back to normal even further. This is explained easily by taking the derivative of the perceptual curves of figure 4 for the two cases that show the repulsion effect. The derivative is the perceptual change per unit of stimulus change and hence describes discrimination of the stimulus. Discrimination is higher than normal where the curves of the figure have a positive slope and lower where the slope is negative.

Perceptual repulsion thus turns out to be in agreement with two generic types of adaptation that, interestingly, have a *contrary* effect on correlations between neural activity: response depression that *decorrelates* cortical responses, and preference attraction that *enhances correlations*. The decorrelation view is one of the major themes in understanding adaptation effects and has received some attention in the literature. We shall next discuss the rationale underlying this view and then turn to correlation enhancement by preference attraction.

(b) *Tuning representations for information maximization*

Over the past ten years, information maximization has become one of the leading paradigms to understand neural representation in primary sensory cortices, especially the primary visual cortex, in terms of an optimal coding strategy. According to this view, neural responses are transformed to reduce their redundancy (Barlow 1989; Atick 1992; Bell & Sejnowski 1997), perhaps also to increase their sparseness (Field 1994; Olshausen & Field 1996), given the statistics of natural stimuli. The cortical network is usually believed to adapt to these statistics by long-term synaptic plasticity. The result would be a maximization of the information represented about a sensory stimulus, given certain bounds on neuronal resources. A similar approach has also been adopted for understanding transformations in subcortical pathways (Atick & Redlich 1992; Dong & Atick 1995; Haft & Van Hemmen 1998; Lewicki 2002).

On a much shorter time-scale, analogous principles of network plasticity or response modulation are often envisaged to underlie adaptation to specific stimuli as described in § 2a (Barlow 1990; Wainwright 1999; Muller *et al.* 1999; Bednar & Mikkulainen 2000). One possibility would be a strengthening of the mutual inhibition between responsive neurons so as to depress any further coincident response and decrease correlations that are induced by that stimulus.

Maximization of the encoded information is a reasonable goal for a channel that transmits messages to a

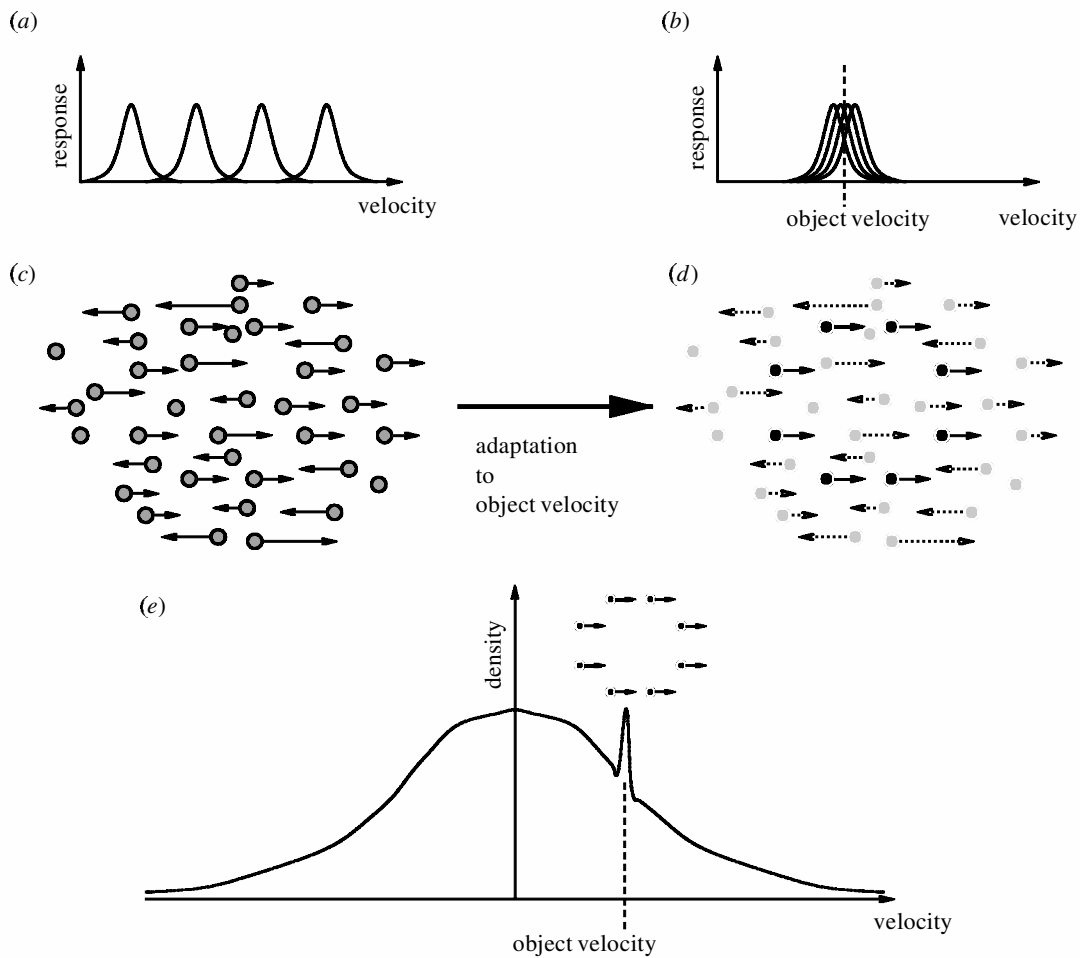


Figure 5. The rationale of object segmentation by velocity-preference tuning (velocity in arbitrary units). (a,b) Schematic representations of the response rates of four cortical neurons as a function of the velocity of a local feature (edge, texture element, etc.) passing their receptive field in an unadapted state (a) and an adapted state (b). Within some region of the visual field a stimulus (c,d) consists of a collection of local features (depicted as dots) moving from left to right and from right to left at various velocities (depicted as arrows). A subset of them is moving at a *common* velocity from left to right. The velocity density (e) of this type of stimulus consists of two components: one symmetrical and one asymmetrical with respect to the two directions of motion. The former derives from the incoherent motion, the latter from the coherent motion and is the statistical signature of a moving object. The adaptive motion system has to detect and tune in to the asymmetrical component of the velocity density. After adaptation of cortical velocity preferences (b), object features are prominent in cortical representation, whereas other features are suppressed (d). The shown stimulus scenario generalizes straightforwardly to motion in two dimensions. (Adapted from Hillenbrand & Van Hemmen (2000).)

receiver. As plausible as this strategy is for a transmitting channel, it is also evident that this cannot be the ultimate goal of sensory processing since sensory processing must eventually lead to behaviour. Behaviour itself is unlikely to preserve the maximum amount of information on the total sensory input. At the end, only what is behaviourally relevant is coded; hence, information is *selected for its behavioural relevance*. The same probably holds for the formation of memory. The principle of behavioural relevance, however, is not captured by maximization of information on elementary stimulus properties. Moreover, it has recently been shown empirically that the intrinsic complexity of a visual recognition task can increase significantly by transforming to statistically less dependent features, even without noise, leading to lower precision in recognition performance (Vasconcelos & Carneiro 2002). It is, therefore, not obvious that neural representations anywhere in the brain are optimized for redundancy reduction or indeed for maximizing the information concerning a sensory stimulus.

In fact, whether elementary sensory information is maximized depends on the *separability* of the brain's processes in *universal representation stages* on the one hand, and more *behaviour-related recognition stages* on the other hand. This two-step strategy is a common design principle for autonomous robotic systems, as it makes the design conceptually transparent. How far this strategy can explain the brain as a biologically evolved system remains an empirical question; cf. Cliff & Noble (1997). The success of explaining the RF structure of neurons in the visual pathway up to simple cells by infomax-like coding principles indicates that some separability exists. One should not expect, however, such principles to prevail throughout the brain; see, for example, Krahe *et al.* (2002).

There is a particular problem with viewing short-term adaptation as a redundancy-reducing process. The behaviourally relevant parts of a stimulus are usually marked by some sort of contingent or coherent structure in the input, that is, some redundancy that exceeds, for a short period of time, the long-term average level. This coherence is

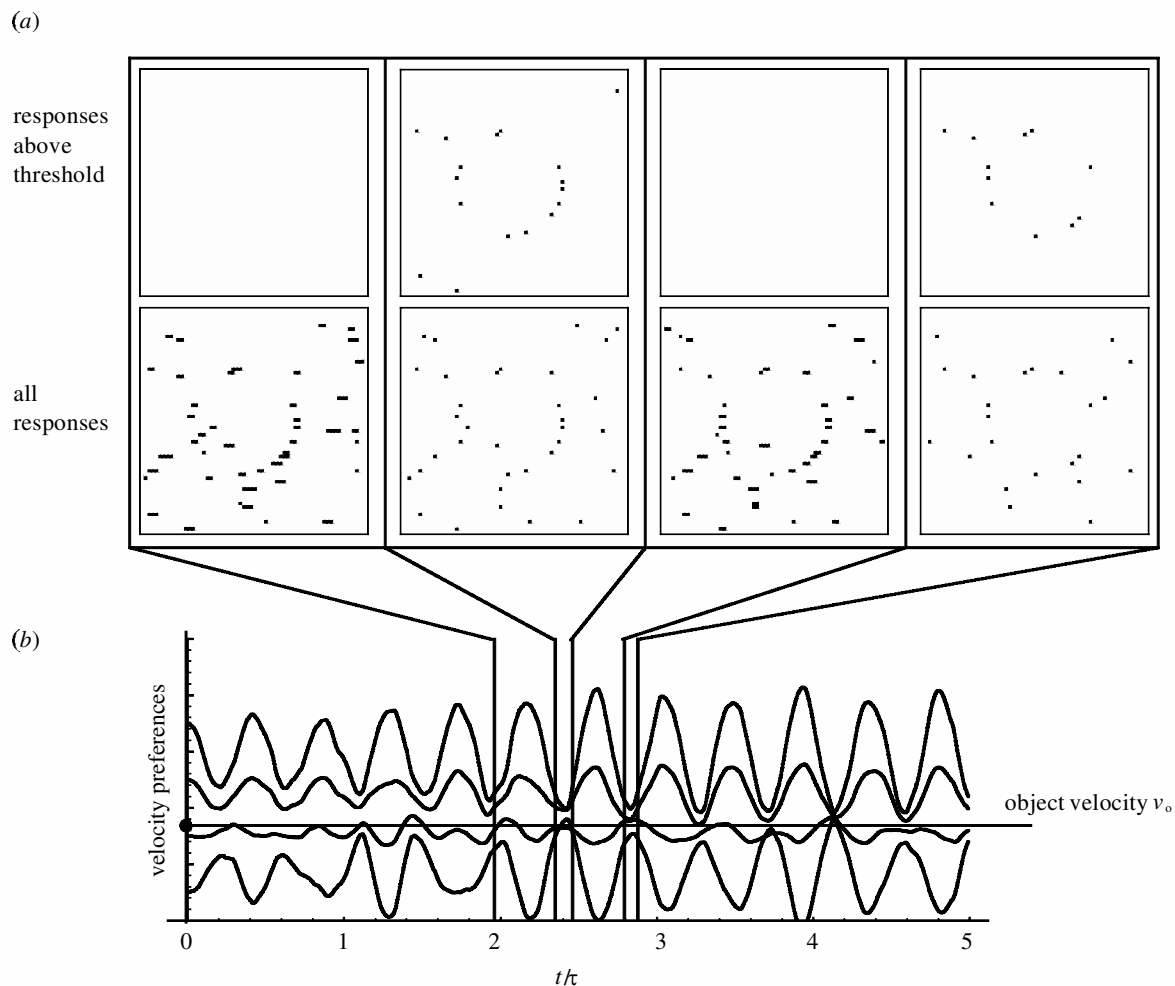


Figure 6. Adaptation dynamics and spatiotemporal pattern of cortical activity in a computer simulation of the corticogeniculate loop. The system is stimulated by 15 dots placed on a circle, all moving at a *common* velocity v_o to the right (object), and 30 dots moving at various random velocities, exceeding or less than the object velocity v_o , either to the left or to the right (background); cf. figure 5. The dynamics of velocity preferences of four representative cortical neurons are shown in (b) (unit of time on the horizontal axis is τ , the rise time of corticothalamic synaptic potentials; the vertical velocity axis has been scaled nonlinearly). The adaptation time-course is oscillatory because of the strong stimulus background. Whenever the neurons' preferences get *close* to the object velocity v_o (horizontal line), object dots elicit a strong response in all cortical neurons that represent their actual retinal positions. The corresponding array of population activity is shown in (a). The lower row of (a) displays *all* responses that occur within the indicated intervals of time; the upper row displays only responses that *exceed* a certain threshold. Nearly all suprathreshold activity is related to object features, demonstrating the segmentation of the object against the background. Spurious suprathreshold activity derives from responses to background dots that by chance have velocities very close to the object's velocity. The suprathreshold activity is oscillatory and synchronous like the adaptation time-course. (Adapted from Hillenbrand & Van Hemmen (2000).)

brought about by the coherence of objects in the outside world.

For instance, the motion of a rigid body induces spatiotemporally correlated signals of local-motion encoding neurons and additional correlations with other stimulus dimensions such as colour. Fading out the associated redundancy within typical object recognition times (hundreds of milliseconds) by rapidly adapting the neural code would render objects invisible in the neural representation. Hence, the behaviourally most relevant aspects of a stimulus would go unnoticed. It therefore seems evident that any redundancy-reducing adaptation can only operate on a longer time-scale than detection of redundant patterns. Moreover, if we do not believe in the rapid formation of a dedicated, behaviourally effective 'grandmother' cell for each contingent conjunction of all correlated stimulus dimensions, it follows that somewhere in the

brain a perceived object must be retained as a highly *correlated* representation.

(c) *Tuning representations to coherent patterns*

We now turn to the alternative scenario of adaptation from § 2a, the attraction of neural preferences towards certain stimulus parameters. We discuss the case of velocity-preference tuning and its possible role in detection and representation of coherent motion. In the light of the results presented by Hillenbrand & Van Hemmen (2000, 2001) and Hillenbrand (2001) and reviewed in § 1b, we propose that this function is supported by corticothalamic loops. As pointed out in § 2b, detection and representation of coherence should operate on a shorter time-scale than any decorrelating mechanism of adaptation.

We argue that the computational goal of velocity-preference tuning is an enhanced representation of behav-

iorally relevant aspects of a stimulus, generally referred to as *objects* and characterized by coherence, and in conjunction with this suppression of less significant aspects, such as neuronal noise and incoherent background motion. The general idea is illustrated in figure 5. It agrees with the preference-attraction scenario of adaptation that is discussed in § 2a.

In Hillenbrand & Van Hemmen (2000) and Hillenbrand (2001) we have analysed a model of the corticogeniculate loop that produces the adaptive behaviour that is sketched in figure 5. When the system is stimulated by a coherently moving object against a background of incoherent, directionally unbiased motion, the neural preferences approach the velocity of the object. This results in an enhanced representation of the object and suppression of background features moving at different velocities—see figure 6.

More specifically, without a background or with just a weak background component in the stimulus, the neural preferences settle in a stationary state close to the object's velocity. As more background is added to the stimulus, persistent oscillations of the neurons' preferences develop. It is important to notice that neuronal background activity, or noise, has the same effect on the adaptation dynamics as incoherent motion in the visual stimulus. The oscillatory time course of adaptation is associated with alternating phases of weak and strong population responses, the strong responses being restricted to object features; cf. figure 6. The dynamic neural preferences thus act as a pacemaker for distributed cortical activity. A periodic time structure is imposed that tends to *synchronize* the firing of cortical cells representing the object. We note that, due to superposition of depolarizing and hyperpolarizing effects of cortical feedback on GRCs, the oscillation period can be shorter than the duration and even the rise time of geniculate postsynaptic potentials. The rise time τ is a free scale parameter in the model. If τ is taken to be 100 ms, the oscillation frequency is *ca.* 25 Hz in the example shown in figure 6.

The model presents an integrated, closed-loop view of the geniculocortical system performing the high-level task of object segmentation. One may, however, ask: is there, apart from theoretical motivation and appeal, any *direct* evidence that similar mechanisms operate in the real system? As far as we know, there is none yet. The model rather offers a template for an alternative computational principle that one may look for when interpreting empirical data on response modulation in functional terms.

Indirect experimental evidence for the model may be seen in diverse phenomena such as visual-motion-induced oscillations of cortical synaptic potentials (Bringuier *et al.* 1997), visual-perceptual stabilization during fixation and the jitter after-effect (Murakami & Cavanagh 1998), percepts of relative motion (Kaufman 1974; Van Essen & Anderson 1990), perceptual velocity repulsion (Clymer 1973; Smith & Edgar 1994; Schrater & Simoncelli 1998), and interaction between stimulus density and speed perception (Watamaniuk *et al.* 1993), all discussed in Hillenbrand (2001).

3. CONCLUSION

We may still have a long way to go to arrive at a computational understanding of the thalamocortical system that

is scaled to its complexity and performance. The concept of object segmentation by tuning in neural preferences has been inspired, in part, by the need to get closer to the processing of behaviourally relevant information in an integrated thalamocortical model.

The modulation of cortical responses in the spatial and temporal context of a stimulus may have various effects on different time-scales and levels of representation. The ultimate goal of sensory coding, however, is to support behaviour. Accordingly, correlated, object-related patterns must be picked up from the sensory input and persistently represented somewhere in the brain. Hence, we have questioned the computational plausibility of redundancy reduction as an effect on a very short time-scale or across all levels of sensory representation.

We have instead argued that responses are modulated so as to enhance object-related correlations and suppress incoherent stimulus aspects, initially at lower or universal levels and persistently at higher or behaviour-related levels of representation. A modulation at the lower levels may be described as a pre-attentive gating. Object segmentation through velocity-preference tuning is a concrete realization, which we propose to be supported by corticothalamic loops.

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REFERENCES

- Alonso, J. M., Usrey, W. M. & Reid, R. C. 1996 Precisely correlated firing in cells of the lateral geniculate nucleus. *Nature* **383**, 815–819.
- Atick, J. J. 1992 Could information theory provide an ecological theory of sensory processing? *Network* **3**, 213–251.
- Atick, J. J. & Redlich, A. N. 1992 What does the retina know about natural scenes? *Neural Comput.* **4**, 196–210.
- Barlow, H. B. 1989 Unsupervised learning. *Neural Comput.* **1**, 295–311.
- Barlow, H. B. 1990 A theory about the functional role and synaptic mechanism of visual after-effects. In *Vision: coding and efficiency* (ed. C. Blakemore), pp. 363–375. New York: Cambridge University Press.
- Bednar, J. A. & Miikkulainen, R. 2000 Tilt after effects in a self-organizing model of the primary visual cortex. *Neural Comput.* **12**, 1721–1740.
- Bell, A. J. & Sejnowski, T. J. 1997 The 'independent components' of natural scenes are edge filters. *Vis. Res.* **37**, 3327–3338.
- Blakemore, C. & Campbell, F. 1969 On the existence of neurons in the human visual system selectively sensitive to the orientation and size of retinal images. *J. Physiol. (Lond.)* **203**, 237–260.
- Blakemore, C., Carpenter, R. H. S. & Georgeson, M. A. 1970 Lateral inhibition between orientation detectors in the human visual system. *Nature* **228**, 37–39.
- Bringuier, V., Fregnac, Y., Baranyi, A., Debanne, D. & Shulz, D. E. 1997 Synaptic origin and stimulus dependency of neuronal oscillatory activity in the primary visual cortex of the cat. *J. Physiol. (Lond.)* **500**, 751–774.
- Campbell, F. W. & Maffei, L. 1971 The tilt after-effect: a fresh look. *Vis. Res.* **11**, 833–840.
- Cliff, D. & Noble, J. 1997 Knowledge-based vision and simple visual machines. *Phil. Trans. R. Soc. Lond. B* **352**, 1165–1175. (DOI 10.1098/rstb.1997.0100.)
- Clymer, A. B. 1973 The effect of seen movement on the apparent speed of subsequent test velocities: speed tuning of movement. PhD thesis, Columbia University, NY.

- Cox, C. L. & Sherman, S. M. 1999 Glutamate inhibits thalamic reticular neurons. *J. Neurosci.* **19**, 6694–6699.
- Crunelli, V. & Leresche, N. 1991 A role for GABA_B receptors in excitation and inhibition of thalamocortical cells. *Trends Neurosci.* **14**, 16–21.
- DeAngelis, G. C., Ohzawa, I. & Freeman, R. D. 1995 Receptive-field dynamics in the central visual pathways. *Trends Neurosci.* **18**, 451–458.
- Dong, D. W. & Atick, J. J. 1995 Temporal decorrelation: a theory of lagged and nonlagged responses in the lateral geniculate nucleus. *Network* **6**, 159–178.
- Dragoi, V., Sharma, J. & Sur, M. 2000 Adaptation-induced plasticity of orientation tuning in adult visual cortex. *Neuron* **28**, 287–298.
- Dragoi, V., Rivadulla, C. & Sur, M. 2001 Foci of orientation plasticity in visual cortex. *Nature* **411**, 80–86.
- Ferster, D., Chung, S. & Wheat, H. 1996 Orientation selectivity of thalamic input to simple cells of cat visual cortex. *Nature* **380**, 249–252.
- Field, D. J. 1994 What is the goal of sensory coding? *Neural Comput.* **6**, 559–601.
- Gibson, J. & Radner, M. 1937 Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies. *J. Exp. Psychol.* **20**, 453–467.
- Godwin, D. W., Vaughan, J. W. & Sherman, S. M. 1996 Metabotropic glutamate receptors switch visual response mode of lateral geniculate nucleus cells from burst to tonic. *J. Neurophysiol.* **76**, 1800–1816.
- Grunewald, A. & Grossberg, S. 1998 Self-organization of binocular disparity tuning by reciprocal corticogeniculate interactions. *J. Cogn. Neurosci.* **10**, 199–215.
- Guillery, R. W. 1995 Anatomical evidence concerning the role of the thalamus in corticocortical communication: a brief review. *J. Anat.* **187**, 583–592.
- Haft, M. & Van Hemmen, J. L. 1998 Theory and implementation of infomax filters for the retina. *Network* **9**, 39–71.
- Hillenbrand, U. 2001 Spatiotemporal adaptation in the corticogeniculate loop. Doctoral thesis, Technische Universität München. <http://tumb1.biblio.tu-muenchen.de/publ/diss/ph/2001/hillenbrand.pdf>
- Hillenbrand, U. & Van Hemmen, J. L. 2000 Spatiotemporal adaptation through corticothalamic loops: a hypothesis. *Vis. Neurosci.* **17**, 107–118.
- Hillenbrand, U. & Van Hemmen, J. L. 2001 Does corticothalamic feedback control cortical velocity tuning? *Neural Comput.* **13**, 327–355.
- Hirsch, J. A., Alonso, J.-M., Reid, R. C. & Martinez, L. M. 1998 Synaptic integration in striate cortical simple cells. *J. Neurosci.* **18**, 9517–9528.
- Huguenard, J. R. & McCormick, D. A. 1992 Simulation of the currents involved in rhythmic oscillations in thalamic relay neurons. *J. Neurophysiol.* **68**, 1373–1383.
- Humphrey, A. L. & Weller, R. E. 1988 Functionally distinct groups of X-cells in the lateral geniculate nucleus of the cat. *J. Comp. Neurol.* **268**, 429–447.
- Jagadeesh, B., Wheat, H. S., Kontsevich, L. L., Tyler, C. W. & Ferster, D. 1997 Direction selectivity of synaptic potentials in simple cells of the cat visual cortex. *J. Neurophysiol.* **78**, 2772–2789.
- Kaufman, L. 1974 *Sight and mind, an introduction to visual perception*. New York: Oxford University Press.
- Koch, C. 1987 The action of the corticofugal pathway on sensory thalamic nuclei: a hypothesis. *Neuroscience* **23**, 399–406.
- Krahe, R., Kreiman, G., Gabbiani, F., Koch, C. & Metzner, W. 2002 Stimulus encoding and feature extraction by multiple sensory neurons. *J. Neurosci.* **22**, 2374–2382.
- Lewicki, M. S. 2002 Efficient coding of natural sounds. *Nature Neurosci.* **5**, 356–363.
- Lewis, J. E. 1999 Sensory processing and the network mechanisms for reading neuronal population codes. *J. Comp. Physiol. A* **185**, 373–378.
- Li, C. Y., Lei, J. J. & Yao, H. S. 1999 Shift in speed selectivity of visual cortical neurons: a neural basis of perceived motion contrast. *Proc. Natl Acad. Sci. USA* **96**, 4052–4056.
- McClurkin, J. W., Optican, L. M. & Richmond, B. J. 1994 Cortical feedback increases visual information transmitted by monkey parvocellular lateral geniculate nucleus neurons. *Vis. Neurosci.* **11**, 601–617.
- McCormick, D. A. 1992 Neurotransmitter actions in the thalamus and cerebral cortex and their role in neuromodulation of thalamocortical activity. *Prog. Neurobiol.* **39**, 337–388.
- McCormick, D. A. & Huguenard, J. R. 1992 A model of the electrophysiological properties of thalamocortical relay neurons. *J. Neurophysiol.* **68**, 1384–1400.
- McCormick, D. A. & Von Krosigk, M. 1992 Corticothalamic activation modulates thalamic firing through glutamate ‘metabotropic’ receptors. *Proc. Natl Acad. Sci. USA* **89**, 2774–2778.
- Marshak, W. M. & Sekuler, R. 1979 Mutual repulsion between moving visual targets. *Science* **205**, 1399–1401.
- Mastrorarde, D. N. 1987 Two classes of single-input X-cells in cat lateral geniculate nucleus. I. Receptive-field properties and classification of cells. *J. Neurophysiol.* **57**, 357–380.
- Muller, J. R., Metha, A. B., Krauskopf, J. & Lennie, P. 1999 Rapid adaptation in visual cortex to the structure of images. *Science* **285**, 1405–1408.
- Murakami, I. & Cavanagh, P. 1998 A jitter after-effect reveals motion-based stabilization of vision. *Nature* **395**, 798–801.
- Murphy, P. C. & Sillito, A. M. 1987 Corticofugal feedback influences the generation of length tuning in the visual pathway. *Nature* **329**, 727–729.
- Murphy, P. C., Duckett, S. G. & Sillito, A. M. 1999 Feedback connections to the lateral geniculate nucleus and cortical response properties. *Science* **286**, 1552–1554.
- Murthy, A., Humphrey, A. L., Saul, A. B. & Feidler, J. C. 1998 Laminar differences in the spatiotemporal structure of simple cell receptive fields in cat area 17. *Vis. Neurosci.* **15**, 239–256.
- Olshausen, B. A. & Field, D. J. 1996 Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature* **381**, 607–609.
- Phinney, R. E. & Siegel, R. M. 2000 Speed selectivity for optic flow in area 7a of the behaving macaque. *Cerebral Cortex* **10**, 413–421.
- Reid, R. C. & Alonso, J. M. 1995 Specificity of monosynaptic connections from thalamus to visual cortex. *Nature* **378**, 281–284.
- Rivadulla, C., Martínez, L. M., Varela, C. & Cudeiro, J. 2002 Completing the corticofugal loop: a visual role for the corticogeniculate type 1 metabotropic glutamate receptor. *J. Neurosci.* **22**, 2956–2962.
- Salinas, E. & Abbott, L. F. 1994 Vector reconstruction from firing rates. *J. Comput. Neurosci.* **1**, 89–107.
- Saul, A. B. & Humphrey, A. L. 1990 Spatial and temporal response properties of lagged and nonlagged cells in the cat lateral geniculate nucleus. *J. Neurophysiol.* **64**, 206–224.
- Saul, A. B. & Humphrey, A. L. 1992a Evidence of input from lagged cells in the lateral geniculate nucleus to simple cells in cortical area 17 of the cat. *J. Neurophysiol.* **68**, 1190–1207.
- Saul, A. B. & Humphrey, A. L. 1992b Temporal-frequency tuning of direction selectivity in cat visual cortex. *Vis. Neurosci.* **8**, 365–372.
- Schrater, P. R. & Simoncelli, E. P. 1998 Local velocity representation: evidence from motion adaptation. *Vis. Res.* **38**, 3899–3912.
- Sherman, S. M. 1996 Dual response modes in lateral geniculate

- late neurons: mechanisms and functions. *Vis. Neurosci.* **13**, 205–213.
- Sherman, S. M. & Guillery, R. W. 1996 Functional organization of thalamocortical relays. *J. Neurophysiol.* **76**, 1367–1395.
- Sherman, S. M. & Koch, C. 1986 The control of retinogeniculate transmission in the mammalian lateral geniculate nucleus. *Exp. Brain Res.* **63**, 1–20.
- Sillito, A. M., Jones, H. E., Gerstein, G. L. & West, D. C. 1994 Feature-linked synchronization of thalamic relay cell firing induced by feedback from the visual cortex. *Nature* **369**, 479–482.
- Singer, W. 1977 Control of thalamic transmission by cortico-fugal and ascending reticular pathways in the visual system. *Physiol. Rev.* **57**, 386–420.
- Singer, W. 1994 A new job for the thalamus. *Nature* **369**, 444–445.
- Smith, A. T. & Edgar, G. K. 1994 Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception. *Vis. Res.* **34**, 253–265.
- Smith, S. & Wenderoth, P. 1999 Large repulsion, but not attraction, tilt illusions occur when stimulus parameters selectively favour either transient (M-like) or sustained (P-like) mechanisms. *Vis. Res.* **39**, 4113–4121.
- Stevenson, S. B., Cormack, L. K. & Schor, C. M. 1991 Depth attraction and repulsion in random dot stereograms. *Vis. Res.* **31**, 805–813.
- Van Essen, D. C. & Anderson, C. H. 1990 Reference frames and dynamic remapping processes in vision. In *Computational neuroscience* (ed. E. L. Schwartz), pp. 278–294. Cambridge, MA: A Bradford Book, MIT Press.
- Van Hemmen, J. L. & Sejnowski, T. J. (eds) 2003 *23 problems in systems neuroscience*. New York: Oxford University Press. (In the press.)
- Vasconcelos, N. & Carneiro, G. 2002 What is the role of independence for visual recognition? In *Proc. Eur. Conf. Comput. Vis.*, vol. 2350 of *Lecture Notes in Computer Science*, pp. 297–311. Berlin: Springer.
- Von Krosigk, M., Monckton, J. E., Reiner, P. B. & McCormick, D. A. 1999 Dynamic properties of corticothalamic excitatory postsynaptic potentials and thalamic reticular inhibitory postsynaptic potentials in thalamocortical neurons of the guinea-pig dorsal lateral geniculate nucleus. *Neuroscience* **91**, 7–20.
- Wainwright, M. J. 1999 Visual adaptation as optimal information transmission. *Vis. Res.* **39**, 3960–3974.
- Watamaniuk, S. N., Grzywacz, N. M. & Yuille, A. L. 1993 Dependence of speed and direction perception on cinematogram dot density. *Vis. Res.* **33**, 849–859.

GLOSSARY

- GRC: geniculate relay cell
 LGN: lateral geniculate nucleus
 PGN: perigeniculate nucleus
 RF: receptive field