

Review

Integrated model of visual processing

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Abstract

Cortical processing of visual information requires that information be exchanged between neurons coding for distant regions in the visual field. It is argued that feedback connections are the best candidates for such rapid long-distance interconnections. In the integrated model, information arriving in the cortex from the magnocellular layers of the lateral geniculate nucleus is first sent and processed in the parietal cortex that is very rapidly activated by a visual stimulus. Results from this first-pass computation are then sent back by feedback connections to areas V1 and V2 that act as ‘active black-boards’ for the rest of the visual cortical areas: information retroinjected from the parietal cortex is used to guide further processing of parvocellular and koniocellular information in the inferotemporal cortex. © 2001 Elsevier Science B.V. All rights reserved.

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Contents

1. Introduction: feedforward models and their limitations	96
2. Retroinjection in lower order areas acting as ‘active blackboards’	97
3. Some experimental support for the model.....	100
3.1. Retroinjection of apparent motion signals.....	100
3.2. Role of feedback connections in figure segmentation	102
3.3. Timing of the effects of feedback connections	104
4. Conclusions	104
Acknowledgements	106
References.....	106

1. Introduction: feedforward models and their limitations

The architecture of the primate visual system has been known since the late 1980s. Information is passed from the retina to the lateral geniculate nucleus (LGN) from which it is sent to area V1 which is linked with area V2 by a very dense set of reciprocal connections [22]. Beyond areas V1 and V2, which are the two largest cortical areas of the primate visual system [21], there is a large number of

smaller cortical areas that contain neurons with selectivities to parameters such as color, depth, direction of motion, etc. . . . [49,53].

Despite this detailed knowledge of the architecture of the visual system, it is still unclear how the analysis performed by neurons located in the different cortical areas lead to an integrated percept in a remarkably short time [47]. The dominant model presently used by neurobiologists follows the steps proposed by David Marr in his famous book *Vision* published in 1982 [25]. David Marr proposed to attack the computational problem posed by artificial and natural vision by distinguishing several levels of computation: the primal sketch, the $2^{1/2}$ D and the 3D

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representation. The primal sketch corresponds to a local and 2D analysis of luminance borders. The next level is the $2^{1/2}$ D sketch that encodes the position and orientation in depth of small surface elements in 3D and the final stage is the 3D representation that corresponds to the representation of objects in three dimensions. Thus, it is a model based on a cascade of filters, that starts from a local analysis and progressively builds up a global 3D representation of the visual scene.

This computational model was inspired by the work done at the time in visual neurophysiology and it, in turn, has had a strong influence on the functional model of the visual system. The echo of David Marr's model in neurobiology is the feedforward model based on the hierarchy of cortical areas of the primate visual system. The hierarchical arrangement of cortical areas (Fig. 1A) was developed by Maunsell and Van Essen [51] who took advantage of the difference between two types of connections between cortical areas, the feedforward connections that carry the information from low order areas to higher order areas and the feedback connections that transfer information in the reverse direction [37].

What was originally an arrangement of the cortical areas and their interconnections based on anatomy is now used as a functional model of the visual system. According to this model, neurons in areas V1 and V2 first perform local computations on a 2D representation of the visual scene and more global 3D representations are assumed to be achieved in higher order areas through a succession of filters corresponding to neurons with more and more sophisticated properties. This model is feedforward in the sense that the selectivity of a neuron in a higher order area is supposed to be constructed by the ordered arrangement of feedforward inputs from lower order areas. An example of such a mechanism is that proposed by Hubel and Wiesel to explain the orientation selectivity of cortical cells in V1 from the ordered arrangement of inputs from LGN neurons [18]. Although it has been shown recently that local cortical inputs also play an important role in shaping the selectivity of V1 neurons to orientation [2,10], there are a number of arguments that suggest that the ordered arrangement of thalamic inputs is the major determinant of the optimal orientation of a neuron in V1 (e.g. [9]). Results from inactivation experiments of feedforward connections also confirm that the ordered arrangement of feedforward connections are important in establishing the receptive field selectivities in higher order areas [4,5]. The best illustration of the feedforward model is provided by neurons in the inferotemporal cortex for which the large sizes and extremely specific selectivities of their receptive fields are assumed to result from the combination of the feedforward inputs from areas V4 and TEO [46].

What happens when a feedforward model is used to process a realistic picture? As soon as the scene is noisy and cluttered, it fails to identify objects and human figures that are easily and instantaneously recognized by the

human visual system [32]. This is due to the separation in a feedforward model between the operations of segmentation, done first with a local analysis at the low levels, and interpretation that is achieved when a more global view of the entire scene is encoded. In other words, segmenting a visual scene first on the basis of local details only works when the object is unambiguous and unique, a rare occurrence in real vision. The failure of feedforward models to achieve proper recognition is due to the fact that occlusions, shadows, reflections, luminance edges and gradients due to lighting, all lead to difficulties in correct segmentation of the objects in the scene, because interpretation of more global representations are not returned to the local level of analysis. One of the main limitation of the feedforward model is therefore that it does not combine a detailed local analysis with a global percept that is necessary to resolve occlusion and lighting artifacts.

2. Retroinjection in lower order areas acting as 'active blackboards'

The way local analysis and global information can be integrated by the visual system is constrained by the limitations of connections between neurons located in the different cortical areas of the visual system. In order to compute interactions between distant regions in the visual field, two sets of connections can be used: the local horizontal connections and the feedback connections. The necessity of computing with high spatial precision and reaching out to distant regions in the visual field is difficult to achieve with horizontal connections within a single cortical area. Areas such as V1 and V2 that contain neurons coding with high precision the visual scene also have very high magnification factors [11,13,38]. This means for example that the axon of a V1 or V2 neuron with a foveal receptive field cannot reach beyond 0.6° away in the visual field (assuming a maximal axon length of 6 mm). Longer distances can be reached in the region of cortex coding peripheral visual field but these do not go beyond a few degrees of visual angle. Thus, by its local horizontal connections, each V1 and V2 neuron is limited to computations within a very local environment and it cannot participate in integration across long distances in the visual field.

Neurons in higher order areas such as MT, V4, TEO, because of their larger receptive fields and the lower magnification factors in these areas [38], can integrate information across long distances in the visual field. However, the selectivities of their receptive fields are more specialized than are those of neurons in areas V1 and V2 that contain a general-purpose representation of the visual field. For neurons in higher order areas, long-distance integration can be properly achieved through horizontal connections for a given aspect of computation corresponding to the major selectivity of the area (like comput-

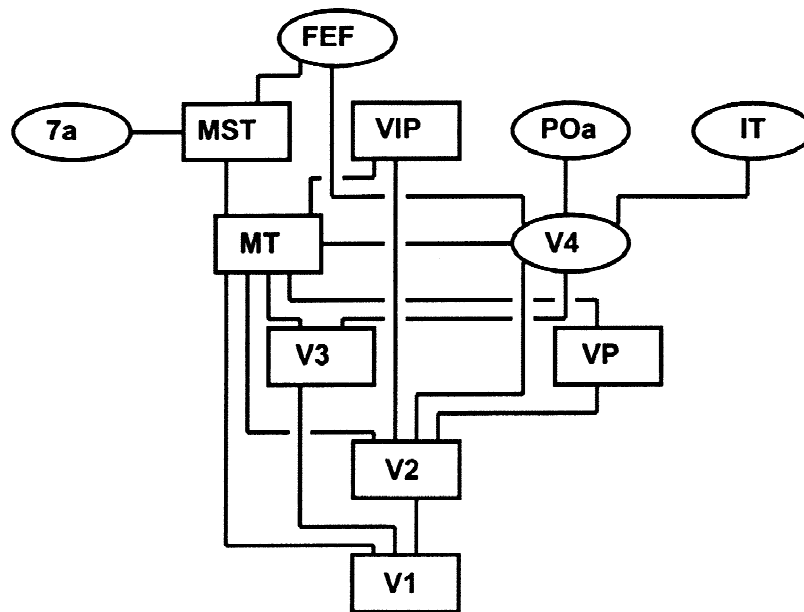
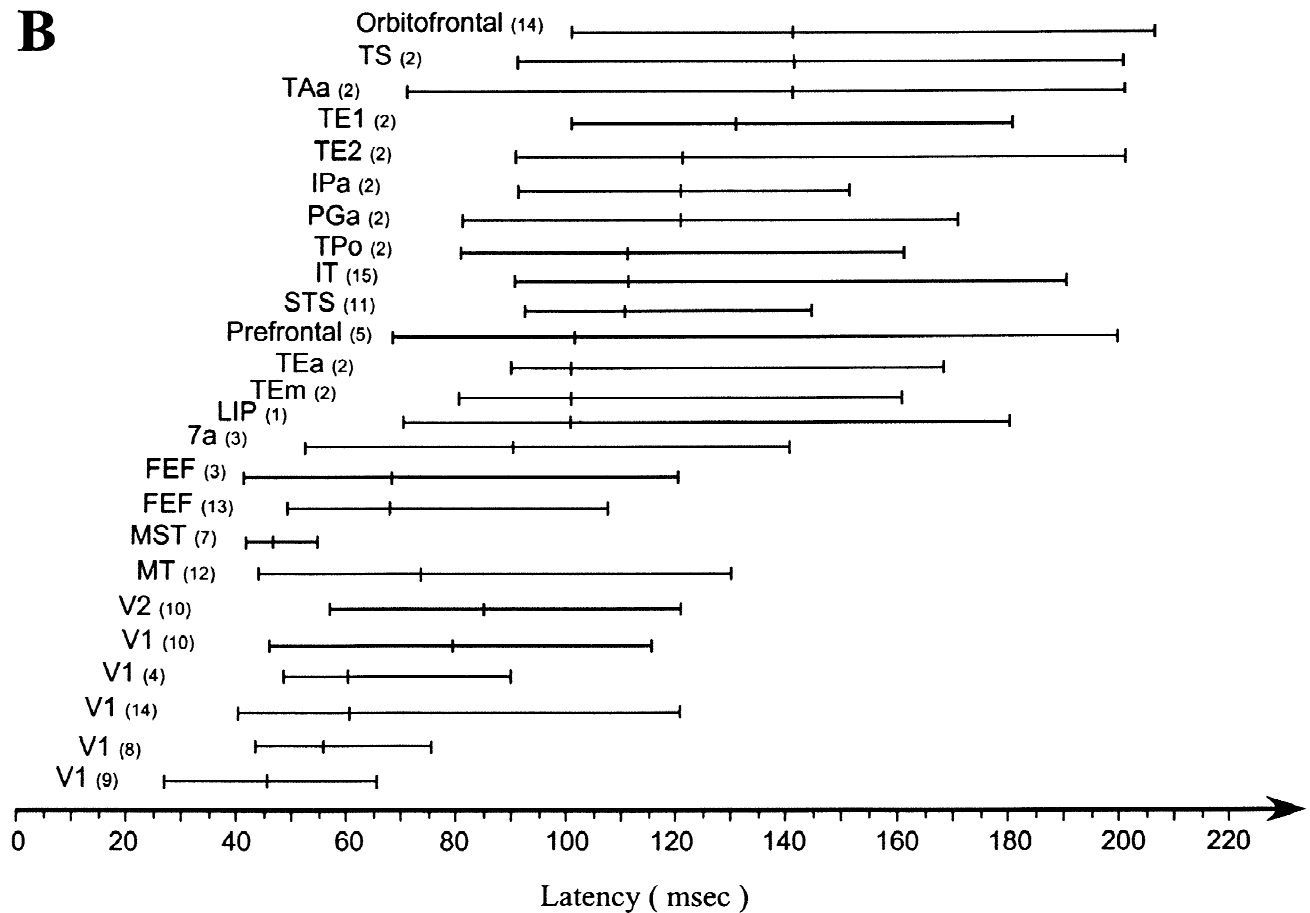
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Fig. 1. (A) Hierarchical organization of cortical areas. This model presents the different cortical areas of the primate visual system staged at different levels according to a simple rule: areas of low-order stages send feedforward connections to the upper levels whereas high-order areas send feedback connections to areas at a lower level (modified from [51]). (B) Latencies of visual responses of neurons in different cortical areas. For each area, the central tick marks the median latency and the extreme ticks the 10 and 90% centiles. Numbers in parentheses refer to bibliographic references given in [4]. Note that the shortest latencies do not always correspond to the lowest stages of the hierarchy. In particular, areas MT, MST, FEF have very short latencies despite their being placed at the highest levels in the earliest version of the hierarchy (Fig. 1A).

ing direction of movement in area MT). However, such computation is impossible when it requires combining neurons with selectivities to different attributes like movement direction, depth, color, shape etc One way to achieve this combination is by exchanging information between neurons in higher order areas coding for different attributes. However, the level of complexity of the computation and the fine grain of the representation that is often needed are probably impossible to achieve with the rather sparse set of such connections (see for example the small number of direct connections between higher order areas of the dorsal and ventral stream [7]).

Another way to resolve this question of computation across long distances in the visual field and different stimulus parameters consists in retroinjecting the results of computations done by neurons in higher order areas through feedback connections to neurons of low order areas such as V1 and V2. Contrary to local horizontal connections, feedback connections have very large convergence regions and can therefore carry information from long distances in the visual field [39], thus achieving the desired goal of integrating global information with local and precise processing. Areas V1 and V2, which contain the largest and most detailed general-purpose representations of the visual field could therefore act as ‘active blackboards’ [31] integrating in their neuronal responses the computations done in higher order areas. Such modifications of responses could in turn change the responses of neurons in other higher order areas that are activated later. Thus, with the idea of retroinjection in lower order areas, it becomes essential to identify which parameters get processed first, since the results of this first computation are likely to influence neurons in many other visual areas.

Retroinjection of information from higher to lower order areas is only possible if the transfer of information can be done sufficiently rapidly, so that the results of computations done in higher order areas can really influence the responses of neurons in areas V1 and V2. It is known that 90% of the information transferred by a neuron is transmitted during the first 100 ms of its response to a visual stimulus [17,48]. So, if the first 100 ms of the neuron response cannot be modified because the information arrives too late through a given set of connections, it is unlikely that much computation can be achieved through interactions carried by these connections.

The possibility of influencing the earliest stages of the responses of neurons in low order areas requires two conditions (1) that some neurons in higher order areas are activated sufficiently rapidly to be able to influence neurons in lower order areas. (2) that feedback connections are sufficiently rapid to delay the information arrival by no more than a few milliseconds.

Because they are located close to the entry point of visual information through the LGN, it is usually assumed that neurons in low order areas (V1 and V2) have shorter latencies to visual stimulation than neurons of areas

located higher in the hierarchy. In an earlier review of the literature [33] and a recent update [4], we showed instead that neurons in several cortical areas are activated very early, practically at the same time as areas V1 and V2. As shown in Fig. 1B, it is clear that there are a number of cortical areas, such as MT, MST, FEF (frontal eye field) and 7a that contain neurons that are activated sufficiently early to influence neurons in areas V1 and V2. It is interesting to note that these areas are in the parietal cortex or, in the case of FEF, in a region of frontal cortex that is heavily interconnected with the parietal cortex. These areas that we called the ‘fast brain’ [33] belong to the dorsal stream or its continuation in the frontal cortex [29,41].

The second requirement, that of the speed of feedback axons to areas V1 and V2 has recently been addressed by Girard et al.: studying the reciprocal connections between areas V1 and V2 in the monkey, they showed that feedback axons are as rapid as feedforward axons and that both are much faster than local horizontal axons [14]. Indeed, the median conduction velocity of horizontal connections in V1 is only 0.33 m/s, a value comparable to that cited by Grinvald et al. when they studied the speed of activity propagating across the surface of the same area [16]. Similarly, the intracellular recordings of Frégnac et al. in cat area 17 also returned median conduction speeds of the order of 0.1 m/s across the cortical surface [3]. Such a slow conduction speed of local axons in cortex limits the type of computation that can be achieved through horizontal connections. To return to the example presented earlier, at that speed, a V1 neuron with a foveal receptive field can directly connect to neurons with RFs located up to 0.6° in the visual field in 60 ms. To reach out to 1° would take approximately 100 ms¹. Given that the average intersaccadic period is of the order of 200 ms and that it is assumed that most information is picked up and processed within this period, such long conduction delays preclude the use of horizontal connections for processing information across long distances in low order areas.

The low velocity of horizontal connections contrasts with those of feedforward and feedback connections that conduct ten times faster [14] because the axons are myelinated and larger in diameter. Given the short distance between areas V1 and V2 [50], conduction times through feedforward and feedback connections between these two areas are very short, of the order of 1 or 2 ms for most axons [14]. It is particularly interesting to note that feedforward axons from area V1 to MT, despite the longer distance, conduct information in the same time as that needed to transfer information into V2 [30]. Thus, the visual cortex is temporally compact with short conduction times between areas distant by several centimeters in the

¹It is important to note that these conduction speeds are median values with large scatters. There are a few myelinated and thick horizontal connections in area V1 that conduct rapidly and tend to be concentrated in layer 4B which is connected to the ‘fast brain’.

brain and several levels in the hierarchy. Assuming that the similarity in conduction time for feedforward and feedback axons demonstrated between areas V1 and V2 also applies for the connections between areas V1 and MT, it appears that information can be transmitted very rapidly from area MT back to V1. Thus, because of the similarity in latencies to visual stimulation in areas V1, V2 and MT and the speed of feedback axons, activity in area MT is in a position to modulate the early part of the responses of neurons in areas V1 and V2 that could therefore act as active blackboards for computations done in area MT.

When studying the temporal aspects of activation of different cortical areas, we made another important observation, that the activity transferred through magnocellular neurons of the LGN reach area V1 some 20 ms earlier than activity transferred from the parvocellular neurons of the LGN [34]. Thus, although M and P channels converge in cortical layers beyond layer 4C [8], M activity precedes P activity in the different layers of V1 and the higher order areas. The early activation of the dorsal stream after visual stimulation (Fig. 1B) most likely results from its almost exclusive drive by the M channel [26] and the high degree of myelination in many areas of the ‘fast brain’. It appears therefore that the first wave of activity that invades the visual cortex following a visual stimulus appearing in the visual scene is carried by the M channel. The characteristics of the M channel (high contrast sensitivity, poor chromatic selectivity, larger receptive fields and lower spatial sampling rate) are well suited for such a first-pass analysis of the visual scene.

A schematic illustration of the model is shown in Fig. 2. The main ideas behind this organization are (1) The first

activity to reach visual cortex is conveyed by the M channel (2) areas of the dorsal stream are activated very rapidly and are thus in a position to influence the responses of neurons in areas V1 and V2 (3) because of the rapid conduction of feedback connections, results of early computations done through this first pass can influence the responses of V1 and V2 neurons in time for the arrival of the P wave of activity that is delayed by 20 ms (4) areas V1 and V2 serve as general purpose representations, or ‘active blackboards’ that integrate in their responses the computations done at higher levels of the hierarchy. This way interactions between coding for different parameters can be computed with high precision and global information can influence local computation in areas V1 and V2 (5) because of the rapid activation of neurons in the dorsal stream, it is likely that they can influence responses of neurons in the ventral stream mainly by retroinjecting information in areas V1 and V2.

3. Some experimental support for the model

3.1. Retroinjection of apparent motion signals

Using fMRI, we recently measured the blood flow changes generated in the human brain by a stimulus composed of a series of Kanisza illusory rectangles, as illustrated in Fig. 3A [43]. The stimulus is composed of eight ‘pacmen’ that rotate by 90° between each frame of the monitor. The left column of pacmen rotate in the clockwise direction and the right column in the anti-clockwise direction. The pacmen are arranged in such a

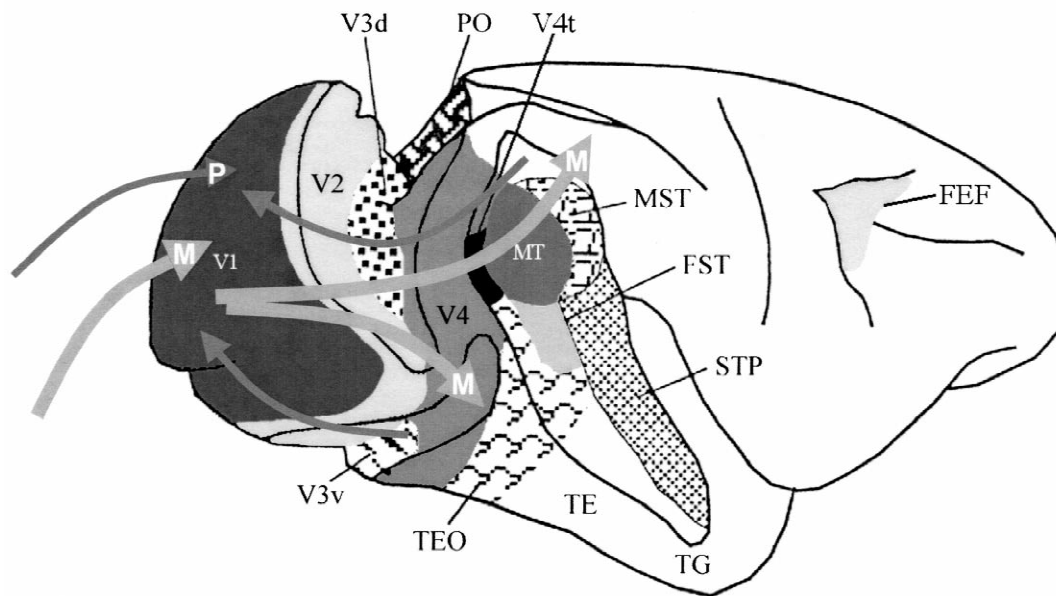


Fig. 2. Integrated model: large arrows represent the activity carried by the M pathway that activates the visual areas first. Feedback connections from the parietal and temporal cortex are supposed to carry signals to be retroinjected in lower order areas in time for the arrival of the P wave of activity illustrated by the narrower arrow.

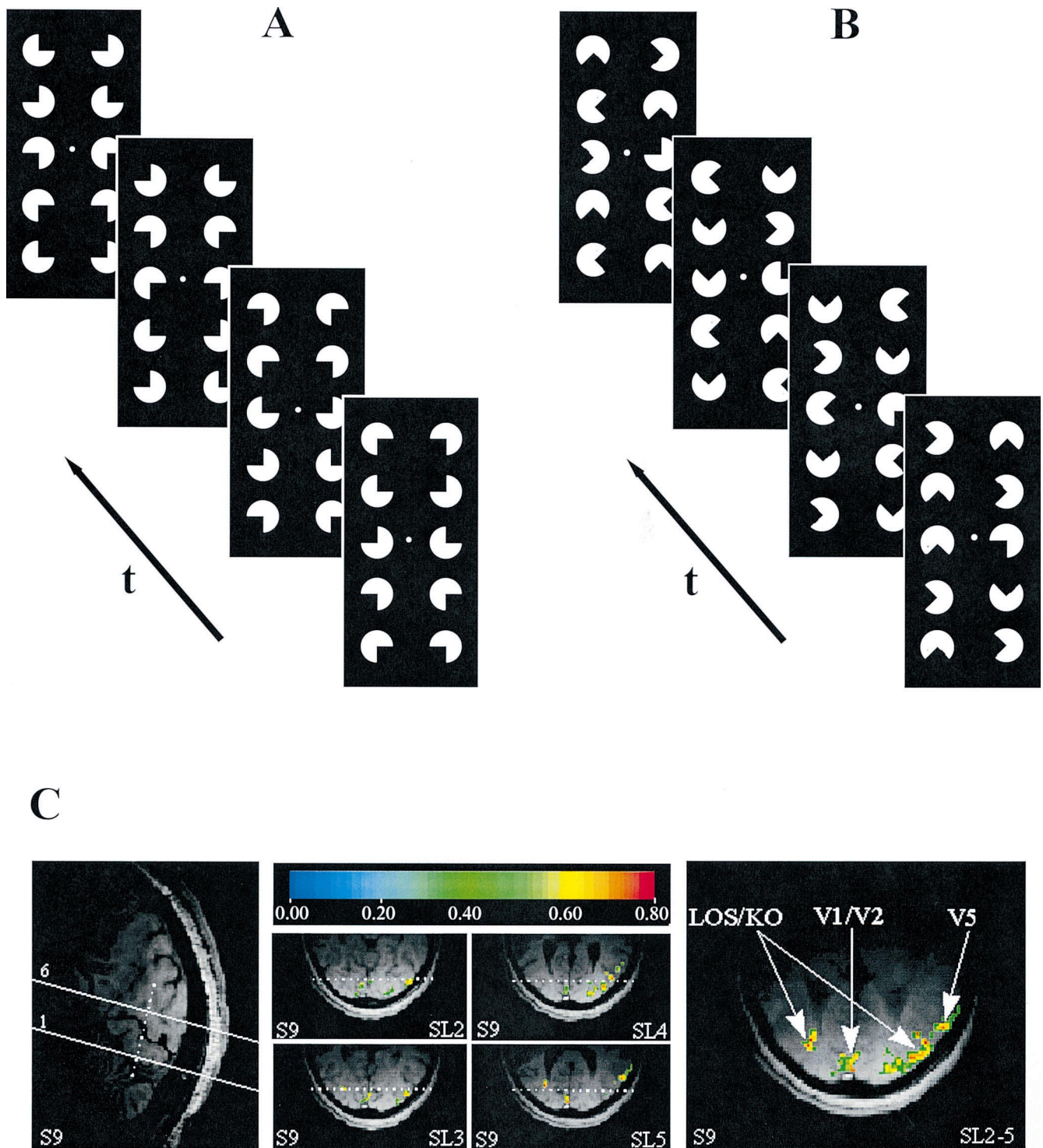


Fig. 3. Activation of areas V1 and V2 by a moving illusory rectangle. (A) Stimulus used to present a moving illusory rectangle. (B) Control stimulus. For each, four successive frames are shown. The saccadic rotation of the pacmen at each frame transition generates the illusion of a downward movement of the illusory rectangle in (A) but not in (B). A small white circle serves as a fixation mark. (C) Typical functional maps obtained in one subject in response to the moving illusory contours compared to the control stimulus. Left, parasagittal image to mark the planes of the scans covering the calcarine sulcus. Center, four functional maps corresponding to different planes. The dashed line serves as a landmark to refer to the parasagittal section. Right, Composite image of the four functional maps showing activation in areas V1/V2, V5 and LOS/KO. Modified from [43].

way that, for each frame, an illusory rectangle is apparent and, for successive frames, the rectangle appears to move downward in a saccadic fashion. This stimulus, originally

described by Ramachandran [36], generates a very strong impression of a rectangle moving downward. The fMRI signal generated by this stimulus presented in block mode

was compared to that generated by the same pacmen that rotated in the same direction but in a desynchronized fashion, thus eliminating the illusory rectangle (Fig. 3B). (The pacmen were also slightly tilted to eliminate the production of moving illusory figures such as scales).

As expected from previous publications, we observed activation in areas V5/MT and areas specific to the presence of a moving object (LOS/KO [15,28]). What was more surprising was the presence of a very strong and reproducible signal in areas V1 and V2 (Fig. 3C; Seghier et al. [43]). Given the relatively large distances between the edges of the pacmen (2° visual angle), it is unlikely that the illusory rectangle activated a large population of neurons in areas V1 and V2 in which the receptive field centers are small, particularly in V1. The probable explanation of this strong metabolic activity in areas V1 and V2 is the following. The signals are generated in neurons of area V5/MT which possess sufficiently large receptive fields to be activated by the moving illusory rectangle and are retroinjected in areas V1 and V2, as proposed in the model presented in Fig. 2.

3.2. Role of feedback connections in figure segmentation

In a different series of experiments [19,20], we tested directly the role of feedback connections by inactivating area MT and recording single unit activity in areas V1, V2 and V3. This time we used a stimulus made up of a light bar moving across a background of white and gray rectangles of same width and variable length (Fig. 4A). This background serves as a mask which completely hides the moving light bar when the contrasts of the bar and the background are equal. When the bar contrast is low but slightly higher than that of the background, a situation that we called low salience, the bar is masked by the background when it is steady and it is made visible by its movement across the background. This situation is particularly interesting because the low-contrast bar is likely to activate mainly area MT that is one of the few areas that respond strongly at low contrast [42]. Thus, at low contrast, when we inactivated area MT we were likely to inactivate a substantial portion of the feedback activity impinging on neurons of areas V1, V2 and V3. In contrast, for high salience stimuli, neurons in these areas are likely to be influenced by the converging feedback inputs from many different higher order cortical areas and inactivating MT only removes a small contingent of the total feedback input.

We used three configurations for the stimulus: the bar moving on a static textured background, the bar moving together with the textured background and the textured background moving alone at the same speed as the bar (Fig. 4A). As illustrated in Fig. 4A, there is no substantial response of the neuron to the moving background alone because of its low contrast. When the bar moves alone on the static background, the response is strong. When the

background moves together with the bar, this response is substantially reduced, because of the inhibitory influence of the surround on the center response. We measured the response strength to the bar alone moving on the static background and the reduction of the response due to the addition of the moving background and we studied how these two measures were modified by inactivation of area MT and the surrounding cortex by cooling [6]. As illustrated in Fig. 4A for a V3 neuron, the response to the bar moving on a static background is substantially decreased when MT is inactivated. On a total of 168 single and multiunits, we observed statistically significant changes in response in 40% of the sites and these changes were decreases in 84% of the cases. This suggests that, for most neurons in low order areas, feedback connections potentiate the responses to activation of the receptive-field center. Other investigators have reached a similar conclusion [40,52]. The average percent change in response strength, measured over the 118 neurons which displayed response decreases is 32.6%. This means that for 70% of recorded neurons in areas V1, V2 and V3, on average one third of their response to a single moving bar is due to the influence of feedback input from area MT. As observed in Fig. 4B, there is a nonsignificant tendency for the change to be stronger for low salience stimuli. Similar results were observed in areas V1, V2 and V3 [6].

Compared to the observations done with a bar moving on a static background, there was a stronger dependence on salience of the effect of MT inactivation on the suppression induced by the moving background on the response generated by the moving bar. This is illustrated in the example in Fig. 4A: during cooling of MT, the response to the bar is no longer substantially suppressed by the moving background, as can be seen by comparing the response to the bar alone and to the bar and background moving together. For the population of 71 neurons in V1, V2 and V3 that showed background suppression, inactivation of MT decreased the background suppression and the effect was most marked at low salience (Fig. 4C). Thus, at low salience, the average background suppression changes from 68 to 17%, which means that the surround suppression was almost completely abolished by MT inactivation. In contrast, only a small decrease of the background suppression was observed when the salience of the stimulus was medium or high. This most likely results from the fact that stimuli at low salience are more likely to activate principally area MT and surrounding areas of the superior temporal sulcus, whereas stimuli at medium and high salience probably activated many other cortical areas in addition. Thus removing the input from MT to neurons in areas V1, V2 and V3 would have a smaller effect at medium and high salience than at low salience, probably explaining the important difference observed between salience levels. Similar effects were observed in areas V1, V2 and V3 [6].

The strong reductions at low salience of the response to

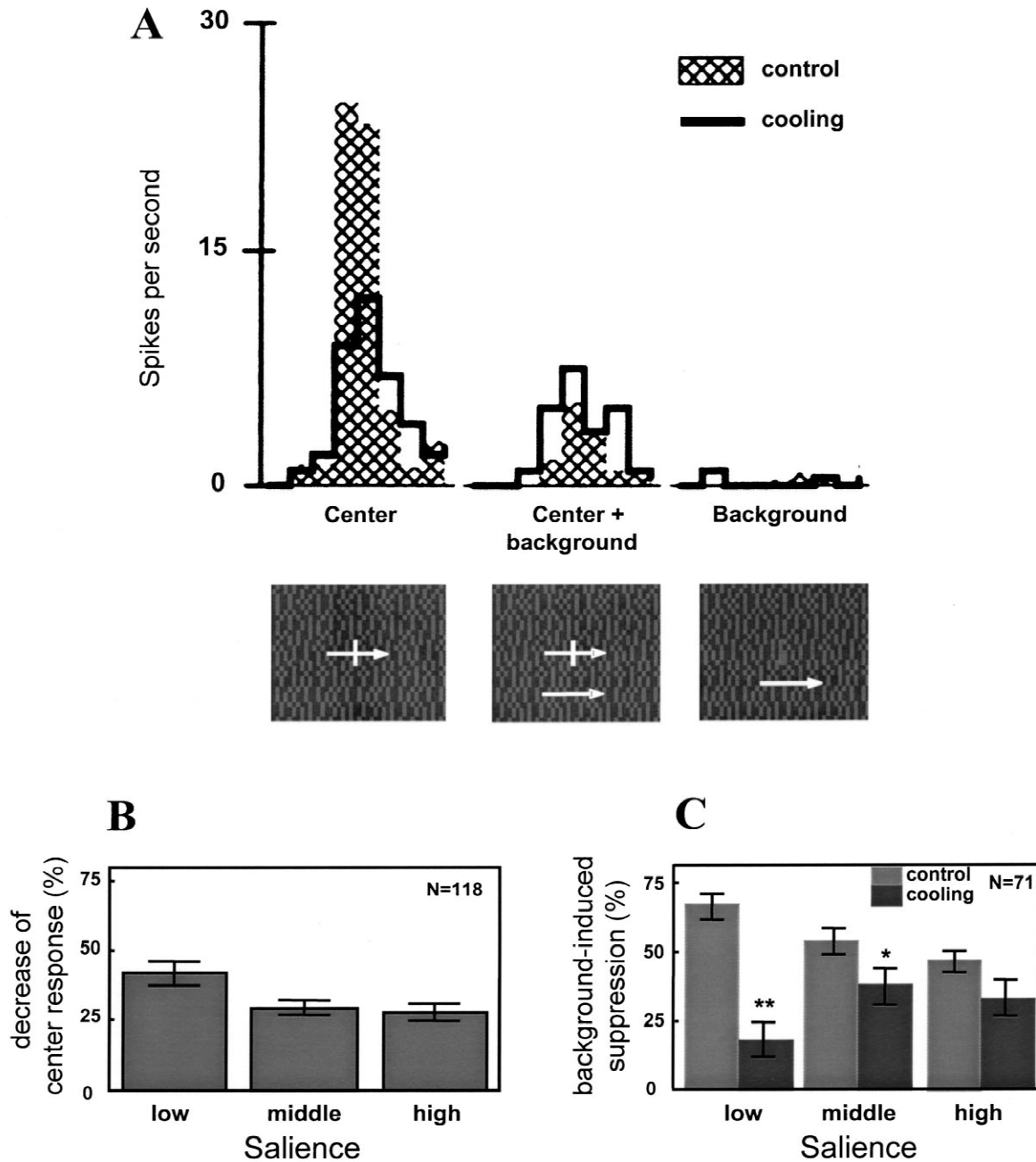


Fig. 4. Effect of cooling inactivation of area MT on the responses of neurons in lower-order areas. (A) Responses of a V3 neuron to a light bar moving across the receptive field center during control and cooling of area MT (modified from [20]). The set of histograms labeled Center correspond to the responses to the bar moving across the static textured background (see stimulus below). The response of the neuron is strongly diminished by MT inactivation. The set of histograms labeled Center+background correspond to the responses recorded when both the central bar and the textured background are moving together. The response during control is much weaker than that to the center stimulus, due to the strong inhibitory effect of the surround mechanism. On the contrary, during cooling of MT, the response to Center+background is only marginally weaker than to the center stimulus. Thus, the inhibitory action of the surround is diminished by inactivation of MT. The right set of histograms shows that there is no response to the movement of the background stimulus alone. (B) Average percent decrease of neuron responses in areas V1, V2, V3 to the bar on static background during MT inactivation for different amount of salience of the center stimulus compared to the background (bars correspond to S.E.M.; the salience corresponds to the ratio of the contrasts of the center bar and the background see [20] for definition; modified from [6]). This shows that at low salience about 40% of the response to the center bar is under the control of feedback connections from MT. (C) Percent suppression of the center response by the moving background for neurons in areas V1, V2, V3 (modified from [6]). Note that at low salience there is an almost complete disappearance of the suppression when MT is inactivated. This means that at low salience the major part of the surround suppression is under the control of feedback connections from MT.

the bar moving on a stationary background and of the suppression by the moving background suggest that feedback from area MT potentiate both the mechanisms of the excitatory receptive field center and of the inhibitory surround. As illustrated elsewhere [6], this leads to an increase in the capacity of neurons in areas V1/V2/V3 to differentiate a faint stimulus moving on a textured background. This is due to the fact that the feedback dramatically increases the difference between the responses of most neurons to a bar moving on a stationary background and those to the same bar moving together with the background. For this reason we concluded that retroinjection by feedback connections plays an important role in figure segmentation in low order areas, because it combines a global analysis to the detailed representation characteristic of the blackboard areas V1 and V2 [6,20].

3.3. Timing of the effects of feedback connections

Given the importance for feedback actions to influence the early part of the response, we investigated the temporal aspects of the effects of inactivating area MT on the responses of neurons in areas V1, V2 and V3. Because of the small number of stimulus repetitions and the variability of neuronal responses, it is in general impossible to assess, for a given unit, the latency at which the effects of MT inactivation become statistically significant. For this reason, we pooled the responses of 51 neurons which showed a significant response decrease to the moving bar during MT cooling. We normalized the response of each neuron with respect to its maximum and estimated its latency. After aligning all the neurons at the same latency, we computed the averaged response to the moving bar in the control situation and compared it to the average response obtained during MT inactivation. The result showed that a statistically significant difference was already present during the first 10 ms bin following the beginning of the response [19]. This means that, for a moving bar, the effects of feedback connections on neurons in V1, V2 and V3 are not delayed with respect to the beginning of the response.

This group result was consistent with the effects seen on individual cases for which the response decrease was observed at the very beginning of the response. It was particularly interesting to observe the effects of MT inactivation on the responses to the moving bar of a few neurons with a relatively high spontaneous activity. MT inactivation did not change the spontaneous activity but reduced the response of the neurons as soon as it started to respond to the stimulus entering the receptive field center [19]. This result was unexpected because the aggregate receptive field (or combination of RFs; [27]) of the MT neurons projecting to a given neuron covers a much wider region of visual field than the receptive field center of the neuron under study [39]. Thus, when a bar moves across the visual field, it activates first the RFs of neurons that

send feedback connections to the recorded neuron. If feedback connections acted in a linear fashion, this should result in effects of MT inactivation on the spontaneous activity of the neuron before it starts to respond to the bar crossing its RF center. The lack of effect on spontaneous activity and the specific effect of MT inactivation on the visual response observed in our results strongly suggests that feedback connections modulate in a non-linear fashion the activity of neurons that result from the ordered inputs through feedforward and horizontal connections. As mentioned earlier [4], such a non-linear effect of feedback connections could also explain the lack of responses of V2 neurons when V1 is inactivated, despite the strong residual activity in area MT and the substantial feedback input from MT to V2 neurons. One of the possible mechanisms of the non-linear potentiation of the center and surround mechanisms by feedback connections is that they act directly on the contrast gain control of neurons in lower order areas.

To be really convincing, the lack of delay of feedback inactivation should be demonstrated on the responses to flashed stimuli because the onset of the flash provides a common time reference to neurons in all visual areas. We flashed small stimuli confined to the receptive field centers of neurons in areas V1, V2 and V3. As for the responses to moving stimuli, we normalized and aligned the responses to their onsets and compared the responses before and during cooling inactivation of area MT. The results are shown in Fig. 5 for the neurons showing a response decrease to the flash during inactivation of area MT. Here again, it is clear that the effect of MT inactivation are not delayed with respect to the response onset. Finally, we checked that the neurons which showed effects of MT inactivation did not belong to a category of neurons with particularly long latencies. This was not the case and there was no difference in latency distribution between the neurons showing an effect of MT inactivation and those showing no effect [19]. In fact, some neurons with very short latencies in layer 4B were strongly influenced by inactivation of area MT.

4. Conclusions

Our results, therefore, are in keeping with a rapid effect of feedback connections on the responses of neurons in lower order areas. Furthermore, the results on background suppression (Fig. 4) confirm the idea that feedback connections play a role in carrying global information to the local computations done in areas V1 and V2. Further support for the integrated model come from reports from other groups. Thus Sugase et al. showed that the amount of information carried by neurons in IT cortex increases more rapidly for global differences (for example a simple shape versus a face) than for finer differences (like faces with different mood expressions or belonging to different people) [44]. Such a result is in keeping with the model

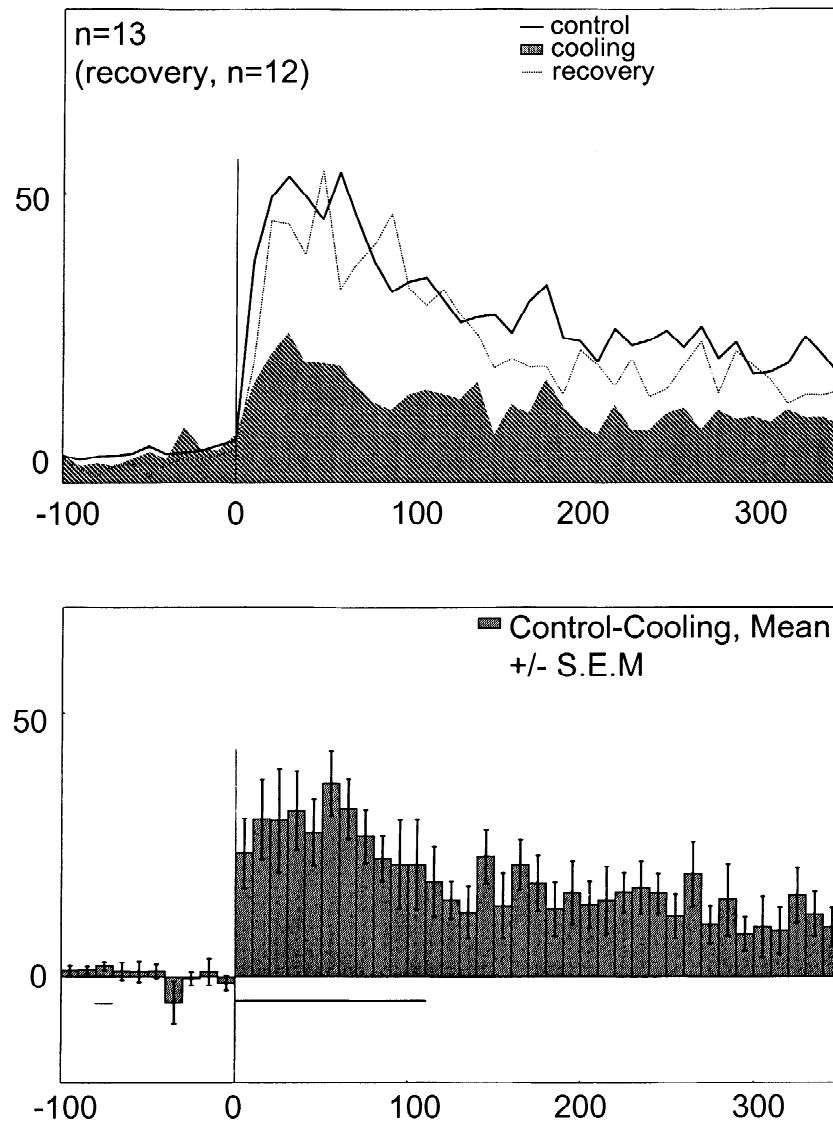


Fig. 5. Timing of effects of MT inactivation on the responses to flash for neurons in areas V1, V2 and V3. Responses have been normalized to the peak of the response and aligned to the response onset. The upper set of curves shows the average response of neurons showing response decrease to a small stimulus flashed in the RF center and how this response is modified by the inactivation of area MT. The histogram below presents the mean difference between control and cooling responses. The bars below the histogram indicate the level of statistical significance for the period before and the first 100 ms after the stimulus onset. It is clear that a statistically significant difference is present at the first 10 ms bin after response onset. Modified from [19].

presented above that suggests that global information is processed first. A similar precedence of global versus fine discriminations has also been recently reported in the olfactory system [12], so the early processing of global information may constitute a general organization principle in the central nervous system.

Interesting examples of rapid global-to-local interactions have been provided by the results of Sugita [45] and more recently by Gilbert et al. [1]. Both papers demonstrated that some neurons in areas V1 and V2 respond to a moving bar occluded by a gray patch when the patch is perceived by stereoscopic vision as placed in front of the two inducers on either side of the patch, and not when the patch is perceived as located beyond the inducers. Such

highly sophisticated responses of neurons in areas V1 and V2 necessitate complex calculations involving precise global-to-local interactions across long distances in the visual field. Both papers noticed that there was no delay in the response to the occluded bar compared to the response to the unoccluded bar, suggesting a very rapid computation that may involve retroinjection through feedback connections instead of horizontal connections. Recording responses of neurons in areas V1 and V2 to illusory contours, Lee and Nguyen [24] found an earlier activation in V2, suggesting that responses to illusory contours in V1 are due to feedback activation from V2.

Another recent report suggests that retroinjection into areas V1 and V2 may be essential for conscious visual

perception (see also [23]). In a coupled transcranial magnetic stimulation (TMS) of areas V1/V2 and MT, Pascual-Leone and Walsh demonstrated that awareness of moving phosphenes induced by MT stimulation was destroyed by subthreshold TMS stimuli applied to areas V1/V2 5–40 ms after MT stimulation [35]. One interpretation of this finding is that the first TMS pulse activates MT neurons that send information back to areas V1 and V2 and that these areas in turn transmit properly organized signals to other areas that lead to the conscious percept of moving phosphenes. When neurons in areas V1/V2 are stimulated by the second TMS pulse at the time they receive feedback signals from MT, they are unable to produce the appropriate spatio-temporal distribution of activity to generate, with activation of other areas, a conscious percept of moving phosphenes.

To summarize, I propose an integrated model that uses the asynchronous transfer of information in the geniculocortical connection and the rapid activation of the dorsal stream by the M channel to generate a first-pass analysis of the visual scene. Through the rapid activation of feedback connections, the computations done at a more global level can be retroinjected into the general purpose areas V1 and V2 that act as active blackboards. Thus, contrary to the feedforward model, it is global-to-local and most likely 3D to 2D (the system sets up rapidly the surfaces in 3D space instead of fully analyzing the 2D scene first). The model makes a number of testable predictions: (1) some aspects of global analysis precedes local analysis (2) global 3D context should influence responses at early stages of the neural responses (3) since this first analysis is done by the M stream, it should remain robust at low contrasts and be disturbed in conditions of isoluminance

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