Archives Italiennes de Biologie, 145: 251-262, 2007.

INPUT-OUTPUT TRANSFORMATION IN THE VISUO-OCULOMOTOR LOOP: COMPARISON OF REAL-TIME OPTICAL IMAGING RECORDINGS IN V1 TO OCULAR FOLLOWING RESPONSES UPON CENTER-SURROUND STIMULATION.

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INTRODUCTION

To adapt our sensitivity to the ever changing luminance or contrast levels of natural scenes is a fundamental aspect of early visual processing. This process is called contrast gain control (1, 22) and is also involved in keeping neuronal selectivity independent upon contrast as well as to improve neural coding efficiency. One important aspect of contrast gain control is contextual dependency: contrast gain of the central receptive field varies with peripheral inputs from outside the classical receptive field (11, 19, 25, 27). These contextual modulations are subtended by lateral interactions, as reported at many levels of the visual system as well as behavioral output. At neuronal level it has been shown in monkey V1 cortex that classical receptive fields are surrounded by a modulatory region (18, 19). Several psychophysical studies demonstrated as well a modulation of contrast detection threshold by surrounding inputs. These modulations depends upon the distance, orientation and alignment of the peripheral inputs (13, 25, 26). In the same vein, we investigated contrast gain control and surround dynamics at behavioral level, using reflexive tracking eye movements initiated at ultra-short latency in humans (7) and monkeys (6). We introduced the concept of a behavioural receptive field whose properties depend on stimulus contrast and lateral interactions. To investigate the hypothesis that intracortical horizontal connections are involved in such contextual modulations (9, 14), we investigated the surround influence on contrast response function (CRF) of large V1 populations. Optical imaging of voltage-sensitive dyes (VSD) allows us to study the real time synaptic population activity in V1 in response to local stimuli of various contrast and the effect of lateral interaction. Herein, we study the role of the interactions between horizontal spread and feedforward input of increasing strength (contrast) in shaping the ocular following response (OFR). OFR provides a behavioural output that, in monkeys, reflects the neuronal activity at an integration stage (areas MT/MST) that collects motion information from large population of retinotopically organized V1 neurons.

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MATERIAL AND METHODS

Voltage Sensitive Dye Imaging

We recorded population activity in V1 using optical imaging of voltage sensitive dyes (28) on one macaque rhesus monkey (*macaca mulatta*). A first surgery was done to insert (i) a head-holder to block the monkey's head, (ii) a scleral search coil to record the position of the right eye using the magnetic search coil technique and (iii) a recording chamber on the skull, above the primary visual cortex. After training of the monkey for fixation, a second surgery was performed: the dura was resected and replaced by an artificial transparent one (4). During extrinsic experiments, the cortex is stained with a voltage sensitive dye (RH-1691, (28, 31)) which, when enlighten with a red (630 nm wavelength) light, emits a fluorescence signal which is linearly dependent of the membrane potential of the stained cells.

During all trials, the monkey was required to fixate a red fixation dot. After 500 ± 100 ms, stimulus appeared for 600 ms in the near periphery of the visual field. The fixation dot was dimmed 200 ms after stimulus offset. Stimuli were displayed on a Viewsonic P225f monitor (22 in, 100 Hz) and generated by a VSG 2/5 graphic card (Cambridge Research Systems). The optical recording started 150 ms before stimulus onset and finished 200 ms after the stimulus was turned off. Data were collected using a Dalstar CCD camera (configured on 512*512 pixels resolution, 110 Hz framerate) operated by Imager 3001 computer and VDaq program (Optical Imaging Inc.). Experimental paradigm, recordings of eye movements (Sampling rate: 1 KHz) and the on-line control of the monkey's behaviour were managed by REX software (16).

Data analysis

For individual trials, optical responses were divided by their values before stimulus onset ("frame0 division"). To extract the evoked response from baseline activity, trials were divided again by a no-stimulation condition response ("blank division", (5)). The obtained measure reflected the fluorescence variation over space and time (F/F). To avoid low frequency physiological noise fluctuations, responses had also been detrended.

All VSD responses were then averaged over a Region of Interest located at the retinotopic cortical projection of the central part of our stimulus (Fig. 1A, first frame). To determine response latency, a fit with a "double cumulative gaussian (1/rc)" function was applied on the beginning of the response (from 0 to 227 ms, see fitting examples on Fig. 3B).

$$rc = k * \left(1 - e^{-\frac{t-t_0}{\tau_1}}\right) * \left(1 - e^{-\frac{t-t_0}{\tau_2}}\right)$$

Ocular Following Response

We recorded ocular following responses on two monkeys, including the one used in optical imaging. We analysed only the open-loop period of tracking onset, defined as twice the response latency (60 ms) after stimulus onset. Behavioral paradigm has been described in previous publications (7). After linearization of the eye position data, we computed eye velocity profiles to illustrate the dynamics of the ocular responses. Quantitative data were obtained by computing a change of eye position over a 10 ms time window, starting at response onset (60 ms) for each trial. Mean and SD were then computed over about 150 trials for each condition, and plotted again stimulus contrast.

Stimuli

We used drifting sine-wave gratings presented behind a circular aperture. Target was presented at 7 different contrasts: 2.5, 5, 10, 20, 40, 60 and 80%. Lateral interactions were studied using counter-phase flickering gratings of same or orthogonal orientation presented within an annulus aperture at 80% contrast. To test the center-surround interactions we presented these stimuli alone or combined (icons on Fig. 2).

Small stimuli were used for optical imaging experiments, retinotopically adjusted to the visible portion of cortex (2° and 4° for center and surround diameter, respectively). Both stimuli were located in the near perifoveal region of the visual field (1° left, 1° down). Orientation (45° counter-clockwise), spatial frequency (1 cpd) and drifting speed (3 Hz) were optimized to V1 neurons response.

To record ocular following responses, we needed much larger stimuli which are able to drive strong reflexive tracking eye movements. We fixed the central drive stimulus diameter at 20°, according to previous studies defining its optimal size. Counter-phase gratings were presented in the surround, up to a diameter of 40°. Central, driving stimuli were vertical gratings with spatial frequency of 0.23 cpd, temporal frequency of 9.6 Hz (speed: 41°/sec). Surround stimulus was a counter-phase grating of similar spatial and temporal frequency. We used peripheral counterphase grating to have dynamical surrounds without eliciting ocular following. Indeed no net motion vector can be extracted from counterphase gratings.

RESULTS

Lateral interactions

Fig. 1A illustrates the cortical point spread function (15) obtained with a single small drifting patch. Clearly, a local stimulus elicited an horizontal slow spread of activity on the cortical surface that started at the retinotopic representation of the visual stimulus. The activated zone started to grow up about 53 ms after stimulus onset. To further determine the dynamics of center and surround responses and their horizontal propagation, we first compared the responses to 80% contrast center-only

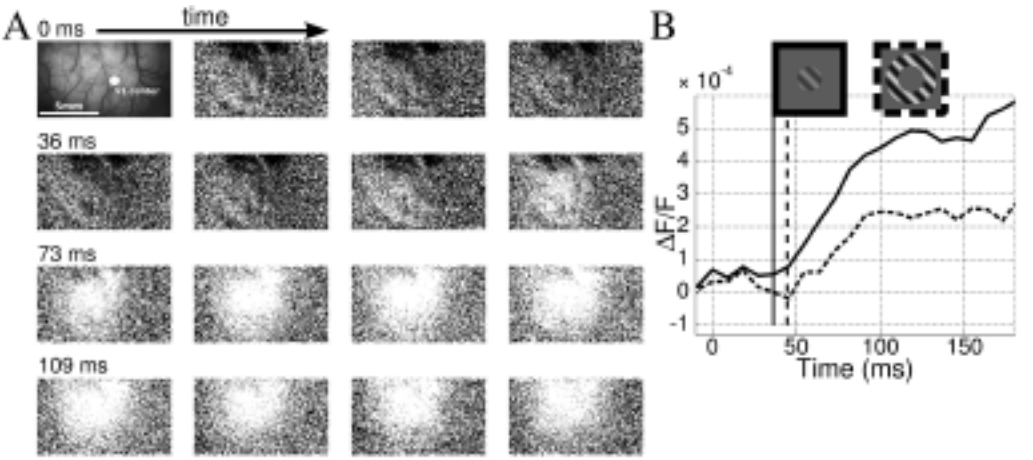

Fig. 1. - *Horizontal propagation of retinotopic activation.*
A: Temporal dynamic of the cortical VSD response to a local stimulation. The response emerges locally and give rise to a large cortical spread of activity over the cortical surface. First frame: imaged cortical area, the white area corresponds to the cortical projection of the center stimulus, scale bar 5 mm.
B: Time course of the VSD responses to the central (solid line) and the surround (dashed) 80% contrast stimuli. Vertical lines indicate response latencies. Response was averaged in the cortical retinotopic representation of the central stimulus. A clear latency shift and amplitude decrease are observed between central and surround stimuli.

and surround-only stimulations in the retinotopic region coding for the central stimulus (Fig. 1B). Responses to surround stimulation started about 10 ms (one temporal frame) later than for center stimulation.

Next,we measured the V1 population response to gratings of different contrasts. The mean optical responses over the Region of Interest corresponding to the central stimulus are plotted against target contrast (Fig. 2A). As stimulation contrast increased, population response amplitude and slope increased whereas latency decreased. Overall, increasing contrast from 2.5 to 80% yielded a four-fold increase in global response amplitude over the first 100 ms. Similar changes with increasing contrast were observed at the behavioral level, when plotting the amplitude of the earliest phase of ocular following against target contrast (Fig. 2B).

To study the effects of lateral interactions on the contrast response function, we measured the response dynamics when central and surround stimuli were presented together. For optical responses, adding a surround stimulation to the center increased the population responses to lower but not higher contrast values. In other words, the modulation amplitude of optical responses over the whole contrast range was decreased, and an offset response was added. Moreover, the overall range of response latencies decreased from 120 ms to 30 ms and became very similar to the range of latencies observed for ocular following responses (Fig. 2D). In ocular following, presentation of a peripheral flickering stimulus alone did not induce any tracking response. Nevertheless, when presented with a central stimulus, flickering surround suppressed the tracking responses to the central grating. The suppression strength scaled with contrast (*i.e.* the higher the contrast, the stronger the suppression, (7)). Thus, the overall range of response amplitudes across the target contrast range was also decreased.

To conclude, the surround effects on the modulation amplitude of responses were very similar for both V1 neuronal population activity and ocular following. However, optical imaging responses were overall stronger in presence of a surround, yielding to an offset in population responses. We further investigated the nature of this increase in global activity and in particular the implication of horizontal connectivity. Given the dynamics of the horizontal propagation, we reasoned that such activity offset resulted from the summation of neuronal activity driven by either horizontal connectivity or feedforward inputs. To evaluate the contribution of horizontal connectivity, we subtracted the surround-only condition to every center+surround trials (Fig. 2E). By doing so, we found that the surround effect was, at first glance, mainly suppressive, quite similar to what was found in OFR.

Latency analysis

One way to probe the possible involvement of horizontal spread from peripheral inputs is to dissect its temporal dynamics. We first quantified the effects of central target contrast on response latencies. Latency of visually-driven population activity, as estimated from fitted optical responses, was largely modulated by center contrast. Latency exponentially decreased as contrast increased, ranging from about 156 ms at

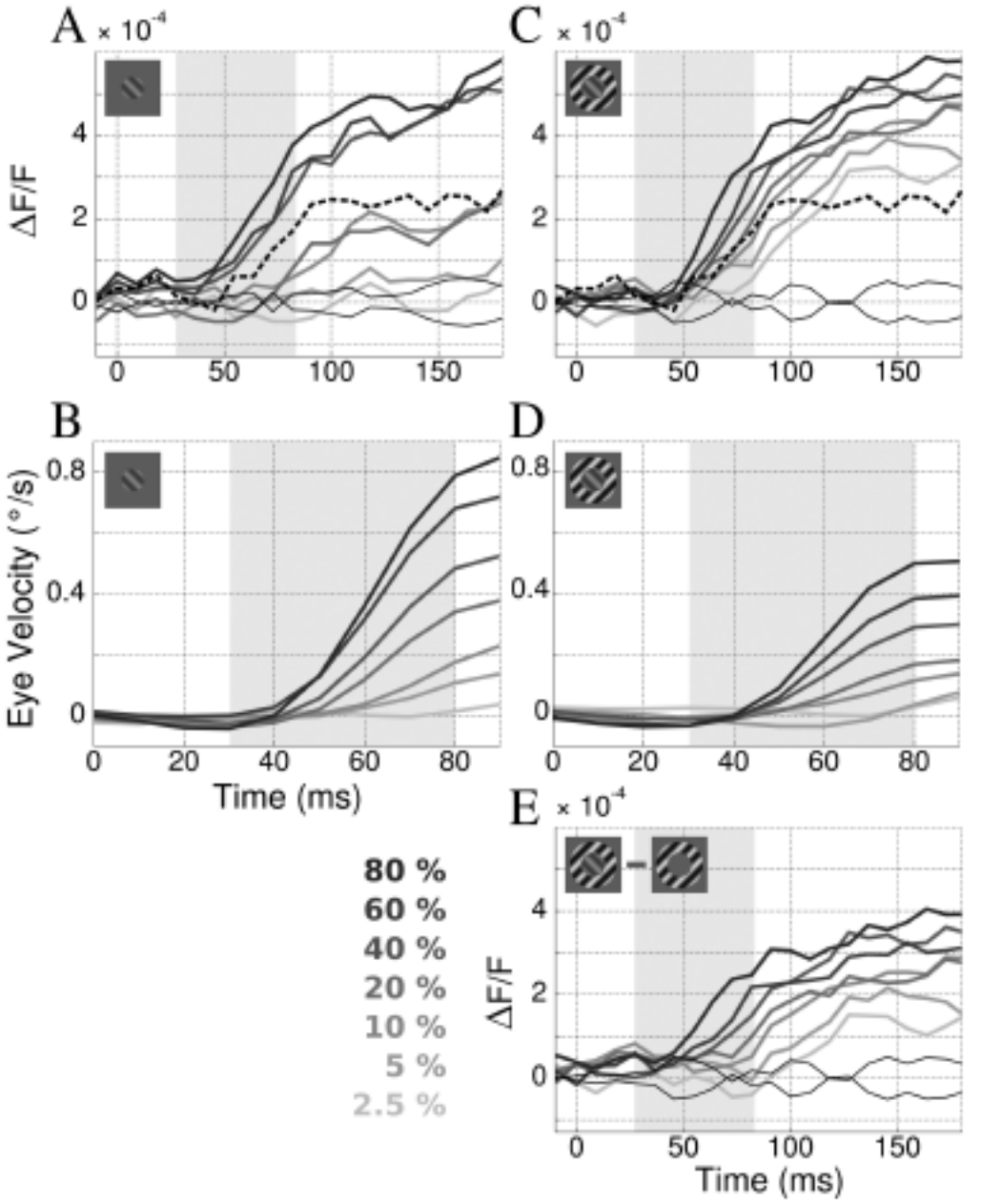

Fig. 2. - *Effect of lateral interactions on the VSD and OFR responses to different contrast*.
Time-course of responses to center-only stimulation, presented at different contrast (gray-scale code) are shown in the left column, for VSD (A) and OFR (B). The effect of lateral interaction with a peripheral stimulus (80% contrast) is shown in the right column for VSD (C) and OFR (D). As in VSD the surround stimulus evokes by itself a response (dashed black curve), we inspected the specific effect on center responses using linear prediction (E). In E, the responses to the center-surround configurations were subtracted by the response to surround stimulus (see Methods). Gray area is underlining similar time window for the OFR and VSD.

2.5% contrast down to about 36 ms with a 80% contrast (Fig. 3, open symbols). The comparison of this curve with surround propagation delay (dashed line) indicates that, for high contrasts (>30%), center response mediated by feedforward inputs lead activation from surround input through lateral interactions. On the contrary, for low contrast values (<30%), the activity generated from the horizontal spread arrived at the retinotopic locus of central target before the feedforward activation from the central stimulus (Fig. 3A). Linear summation of feedforward and lateral inputs would result in a latency of center+surround response that is equivalent to the minimum of these 2 inputs. In other words, for contrast values lower than 30%, center+surround latencies should be equal to surround only and, for values higher than 30%, they should be equal to those observed for center only conditions. We found that for high contrasts center+surround latencies were longer than expected, *i.e.* longer than center-only. For low contrast values, latencies were longer than found with surround-only but shorter than those observed with center-only. The observed latencies (close symbols, Fig. 3) were therefore always longer than the linear predictions suggesting a non-linear integration of feedforward, feedback and horizontal inputs.

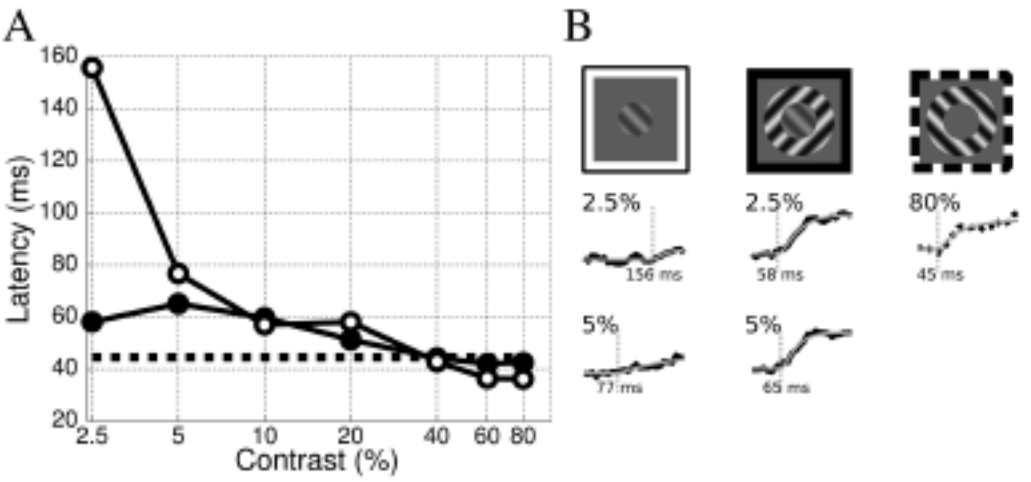

Fig. 3. - *Effect of contrast and lateral interactions on VSD responses latencies*.
A: Responses latencies as a function of contrast for center stimulation (open symbols), center+surround (close symbols) and surround-alone conditions (dashed line, presented at 80% contrast only).
B: Examples of latency measurements (vertical line) are shown for few selected responses, with the fit used to estimate them.

Contrast response function

To quantify the suppressive effects of surround input on feedforward driven response, we measured the contrast response function over the central Region of Interest at different points in time (Fig. 4A,B, gray scale code). This analysis was performed for both optical and ocular responses. Contrast response functions fully

describe the dynamics of cortical gain control and its contextual modulations. Such dynamics are optimally described by (i) contrast threshold above which significant responses can be observed, (ii) a dynamical range over which the response increases with contrast and (iii) a saturation contrast above which different contrast values are not further encoded. Classically, the contrast response function is best fitted by a Naka-Rushton function (2). Such function is characterized by the semi-saturation contrast (c50) and the slope which defines the contrast range to which the system is sensitive (the steeper the slope, the smaller the range).

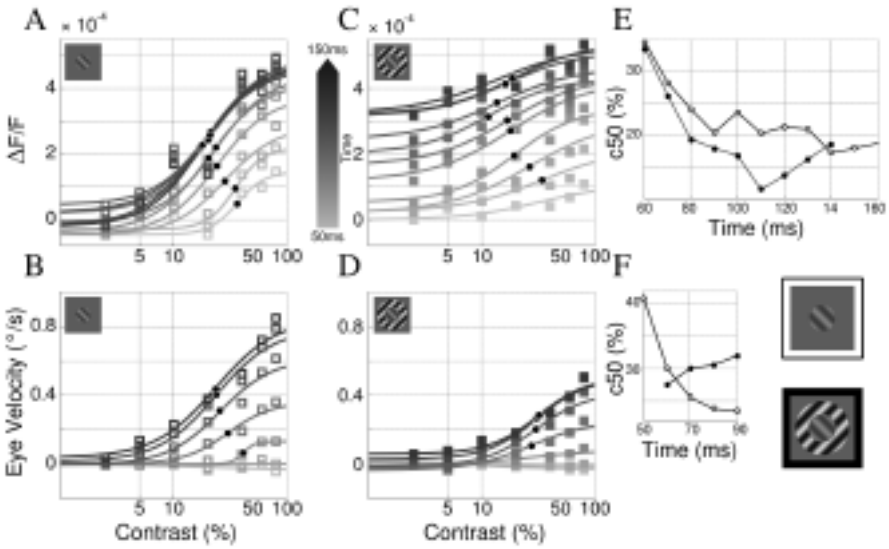

Fig. 4. - *Differences of lateral interactions for VSD and OFR contrast response function*. A-D: illustrate contrast response functions developing over time (gray-scale code) fitted with a Naka-Rushton function ([2]), black dots represent significant semi-saturation constants. VSD response to center (A) or center+surround stimuli (B). OFR responses to center (C) or center+surround stimuli (D). E. Dynamics of constants of semi-saturation for VSD responses (E) and OFR responses (F) to center (open symbols) and center+surround stimuli (close symbols).

With center-only stimuli, the earliest operating range was from 20 to 80%, with response amplitude growing almost linearly between these two values in both OFR and VSD. For the later part of the responses (at 150 ms after response onset), the operating range shifted to 2.5-50%, with saturating response for contrast values above 50% in VSD and to 2.5-80% without saturation in OFR. Fig. 4E,F plots respectively in VSD and OFR the best-fit estimated to c50 over time, showing an exponential decay of population semi-saturation contrast level over a 50 ms time window, going from 35 to 20% (VSD) and from 41 to 23% (OFR).

When a surround was added (Fig. 4C,D), operating range and steepness of the contrast response function was largely affected, the amplitude of responses growing more linearly with contrast. By consequence, population activity exhibited a larger

operating range in the presence of a surround. The same trend was observed for ocular following. However, the temporal dynamics of best-fit estimates of c50 appeared to change differently against contrast for either optical and ocular responses. Fig. 4E illustrates that c50 of responses driven by center+surround conditions fall off exponentially across time, in a similar way to that observed with center-only condition. On the contrary, c50 for ocular following responses stayed constant over time (Fig. 4F), expressing the fact that contrast gain was clamped by adding a flickering surround, as previously observed for ocular responses in humans (7).

Fig. 5B compares contrast response functions for ocular following responses to either center-only or center+surround conditions. One can see that, with surround stimulation, optimal contrast range was only half that observed with the center-only condition and ocular responses to high contrasts were suppressed, the suppression becoming larger and larger over time. Clearly, OFR was dependent upon both the feedforward input but also the surround input directly. To compare with the cortical population response, we tested the linearity of center and surround responses summation via feedforward and horizontal input in V1 by subtracting the surround-only VSD response to the center+surround condition. By doing so, we were able to compare the evolution of center contrast response function over time in both conditions (Fig. 5A, open symbols: center-only; close symbols: center+surround). We found a strong suppression of response amplitude at high contrast, similar to that seen for ocular following responses. However, subtracting the surround-only contribution unveil a striking enhancement of population response amplitude at low contrast, when compared to the center-only condition. This result demonstrates, at population level, a suppressive and a facilitatory effects at high and low center contrast respectively, due to peripheral modulatory inputs.

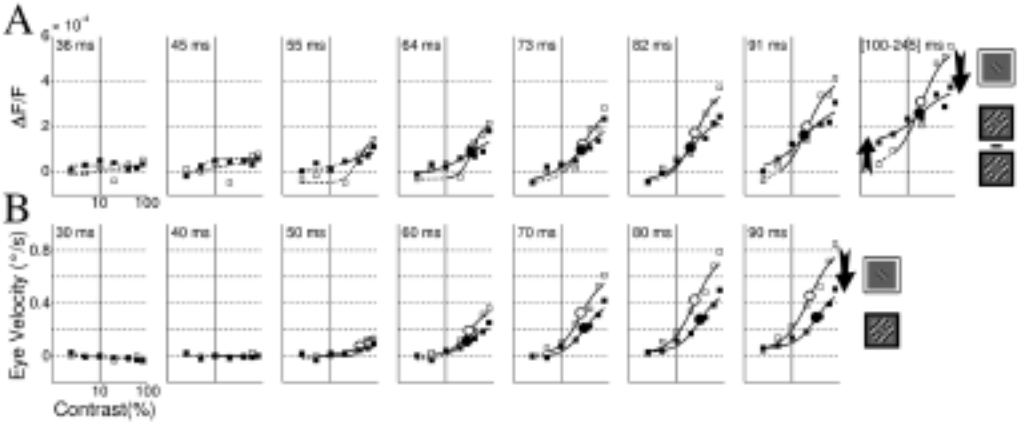

Fig. 5. - *Non-linear dynamics of lateral interactions in the contrast response functions*.
A: VSD contrast response function represented time frame by time frame to center (open symbols) and the linear prediction of the effect of surround to the center stimulus response (close symbols).
B: Dynamics of OFR contrast response function to center (open symbols) and center+surround (close symbols) stimuli. Circles represent semi-saturation constants. We illustrated in dashed curves the VSD or OFR levels before the response latency.

DISCUSSION

The purpose of our study was to determine the role of V1 horizontal connectivity in contextual modulations involved in the cortical contrast gain control observed at the behavioural output level with ocular following responses.

Using a local stimulus, we found a similar dynamical increase in the contrast gain of both ocular and neuronal responses as measured in V1. These results suggest that changes observed at behavioral level are, at least partly, constrained as early as in V1. However, surround modulations were clearly different for ocular and neuronal responses. With ocular following in monkeys, adding a modulatory surround to a local, driving stimulation generates a strong suppression. This suppression is stronger for higher contrasts and grows up over time. With population responses of V1 neurons, the same surround (albeit scaled to fit the imaged cortical surface) induced a slightly different modulatory effect. Suppression was observed for high target contrast (>30%), as found for OFR. However, a significant facilitation of the neuronal responses was observed for low target contrasts (<30%).

Such observation must be compared with the latency analysis, where adding a surround speeds up responses at low contrast but delays them at high contrasts, when compared to center-only responses. Such temporal dynamics might be due solely to the incoming wave of neuronal activity coming from the surround representation which has a fixed contrast value. Assuming a linear summation of center and surround-driven activity, we subtracted this surround-driven responses and then observed that surround stimulation in fact resulted in a general delay of the center+surround responses, observed for all contrasts albeit with different values (5 ms for high contrasts and 20 ms for low contrasts). To summarize, our result can be described as a delayed facilitation for low contrasts and a delayed suppression for high contrasts.

How could we explain both suppression versus facilitation effects and different delays ? For high contrasts, the slow-down of the response to center suggests that the suppression could be due to a fast influence of feedback loop from MT on the feedforward integration (3, 29). Clearly, we saw that the horizontal spread across V1 is too slow to affect the early response of high contrast stimuli. On the contrary, the feedback loop is fast enough (10) even more if we take into account the possibility of a direct thalamic input on MT (30). For low contrasts, yielding to a longer latency of the modulated response, the horizontal spread is already present but hidden by the feedforward input. This interference operated between both inputs suggests a change in the priorities of the cortical integrative resources, leading to a facilitatory modulation (12, 17). Similar dual modulatory influence have already been shown in V1 (19, 24, 27) but also in MT (23), and generates a functional flattening of the contrast response function: low contrasts are boosted and high contrasts are lopped.

These differences exerted by lateral interaction generate as well a different dynamic behaviour of the contrast response function. In OFR, adding a surround stimulus clamps the response function, with a semi-saturation contrast that does not change

with time. In V1, however, the contrast response function is functionally unchanged by the presence of the surround. At which stage of the cortical processing those differences arise? We saw that there is indication that MT have similar dual modulation than what we report here. Furthermore, if MT would generate a change in the contextual modulation of the contrast response function, we would expect to see it in V1 because of the heavy feedback projections. We know that there is a differential projection from MT on MST of cells having particular center-surround organizations (8), and that there is so far no indication of a feedback from MST on V1. We therefore suggest that the contextual change in the contrast response function is happening in the convergence of MT on MST, or in the cortical processing within MST. Alternatively, we cannot rule out the possibility that the effect we observed are not scale invariant, although Barthélemy *et al.* showed it for part of the spatio-temporal scale, albeit in humans (7).

Therefore, our results suggest that the properties of ocular following are the byproduct of a strong interplay between a cortical integration of the visual input in V1, feedback and differential convergence of connectivity from MT to MST. To sort out the functional role of all these connectivity schemes, we need dedicated experiments which would allow us to specifically test each streams independently, taking advantage of the extremely short-latency of ocular following (21) and its fast temporal dynamics (20).

SUMMARY

In psychophysics and physiology, it is well established that lateral interactions are crucial mechanisms to constrain response normalization and contextual modulations. To study the cortical mechanisms involved in the contextual modulation of the behavioral contrast response function, we compared in behaving monkeys the Ocular Following Response (OFR) to V1 population activity measured using Optical Imaging of Voltage-Sensitive Dyes (VSD). If contrast response functions (CRF) to a simple local stimulus are similar in V1 and in the OFR, lateral interaction leads however to quite different modulation at those two levels. At the behavioural level, contrast response function is strongly suppressed by lateral interactions, and this suppression is stronger for higher contrasts. In V1, we showed a slow dynamic of facilitation for low contrasts integration and a fast suppression operating on high contrasts. These modulatory interactions influence differently the contrast response functions, interrupting the dynamic increase of contrast sensitivity in OFR, but not in V1 response. The temporal properties of those effects lead us to hypothesize that horizontal and feedback connectivity have differential effect on low and high contrasts integration in V1. V1 provides then an input to MT whose contextual dependency is not totally determined and must be refined before affecting the behavioural OFR.

Acknowledgements. - This work was supported by the ACI Neuroscience (French ministry of research) and the European Community (integrated project FACETS, IST-15879) who also supported A. Reynaud fellowship. F. Barthélemy was supported by a fellowship from the Fondation pour la Recherche Médicale FRM FDT20051206135

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