J. Physiol. (Paris) 94 (2000) 333–342

PII: S0928-4257(00)01096-2/FLA

The visual cortical association field: A Gestalt concept or a psychophysiological entity?

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Abstract – The receptive field of a visual neurone is classically defined as the region of space (or retina) where a visual stimulus evokes a change in its firing activity. Intracellular recordings in cat area 17 show that the visually evoked synaptic integration field extends over a much larger area than that established on the basis of spike activity. Synaptic depolarizing (dominant excitation) decreases in strength for stimuli that are flashed at increasing distances away from the centre of the discharge field, while their onset latency increases. A detailed spatio-temporal analysis of these electrophysiological data shows that subthreshold synaptic responses observed in the 'silent' surround of cortical receptive fields result from the intracortical spread of activation waves carried by slowly conducting horizontal axons within primary visual cortex. They also predict that a perceptual facilitation may occur when feedforward activation produced by the motion signal in the retina travels in phase in the primary visual cortex with the visually induced spread of horizontal activation. A psychophysical correlate has been obtained in humans, showing that apparent motion produced by a sequence of co-linear Gabor patches, known to preferentially activate V1 orientation selective cells, are perceived by human observers as much faster than non co-linear sequences of the same physical speed. © 2000 Elsevier Science Ltd. Published by Éditions scientifiques et médicales Elsevier SAS

intracellular recording / patch-clamp / synaptic integration field / horizontal connectivity / collinearity / psychophysics / apparent motion / binding

1. Introduction

In his famous 'Traité de l'Homme', René Descartes brilliantly intuited that the brain integrates the visual world information in a serial mode, across a cascade of ordered central representations [9]. His prediction was that, at each step of processing along the central visual pathways, the topography of the visual field representation was homeomorphic to that defined at the retinal level. Three centuries later, numerous studies, among which the pioneering work of David Hubel and Torsten Wiesel [17], showed that an anatomo-functional embodiment of Descartes' view of the visual brain could be found in the retino-geniculo-cortical pathway. The primary visual cortex, whose activation is a necessary step to achieve form perception and figure-ground discrimination, indeed receives ordered neural projections arising from homologous regions in each retina. Each central visual neurone signals by a change in its firing frequency the presence of visual stimuli with specific features (size, contrast, orientation, etc.) in a particular region of the visual field, the so-called 'discharge field' [2, 3, 31]. According to this feed-forward-only projection schema, this sensitivity window on the outside world is defined at the cortical level by the topographical union of the thalamic inputs' discharge fields. The average spatial dimension of this window in cat area 17 is of the order of 1 degree of visual angle for cortical cells whose receptive fields are located around the gaze axis [30].

One of the major problems tackled by electrophysiologists and psychophysicists in the last decade has been to understand which mechanisms, at the synaptic, cellular and network level, underlie the emergence of a global and coherent perception. Such perception arises from a mosaic of sensations transcribed in neural activity terms by a myriad of concomitantly activated discharge fields, which in principle have only a tubular piecewise access to the visual world. The emergence of a unified percept allowing, for example, to identify an object independently of its spatial position in the visual field (spatial invariance), implies the existence of a binding process which links distinct neurones analysing different positions in space. The combinations of 'parts' into a global perceptual entity

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also require that this spatial binding operates at the same time between cells simultaneously activated by each of the components of the 'whole'. Similarly, global motion perception is experienced even if the physical stimulus sequence is a composition of static individual spatial events which individually do not coexist temporally. In that case, as already pointed out by the Gestalt school, the commonality of fate (or destiny) decides of the binding in time.

The studies that we will summarize here describe at the synaptic, cellular and perceptual levels, the spatial and temporal properties of a 'binding' process, possibly of cortical origin. At the neural level, the evidence for such a binding process remains indirect and is based on a detailed analysis of the synaptic background activity, i.e. the network rumour, detected in any given cortical cell. Intracellular electrophysiological recordings in vivo, using sharp and patch electrodes, give access not only to the spiking output response of the cell, classically used to titrate its functional sensitivity, but also to the membrane potential fluctuations. These subthreshold events can be used, in a reverse correlation analysis, to dissociate (demultiplex) the multiple components of the complex processing carried out by the network of cells effectively connected to the cell being recorded. Thus it can be seen that depolarizing and hyperpolarizing events which are too small (500 μV to 10 mV) or of inadequate polarity to evoke spikes, do not solely reflect membrane noise or non-specific tonic background synaptic bombardment. A significant fraction of them also correspond to visually evoked composite excitatory and/or inhibitory postsynaptic potentials, signalling the presence or the extinction of visual stimuli located across a much larger integration zone than the one defined by the classical discharge field.

We show, in cat area 17, that this synaptic integration field can extend up to several tens of degrees [6, 12, 13]. For such cells, at each moment in time, contextual information fed by the cortical network treating the 'peripheral' information will influence the discharge evoked by a test stimulus shown in the centre of the receptive field. A detailed analysis of the arrival times of synaptic events tagged by their retinal origin leads us to propose that this 'lateral' information is presumably relayed by non-myelinated intracortical 'horizontal' axons along the layers of primary visual cortex. We will review at the end of this article the specific consequence, measured at the human psychophysical level, that the propagation of this intracortically relayed activity wave could have on a well documented perceptual illusion, namely apparent motion [22].

2. Methods

2.1. Electrophysiology

Initial anaesthesia was induced by intramuscular injection of Althesin (Glaxo; 1.2 $mL \cdot kg^{-1}$ equivalent to 10.8 $mg \cdot kg^{-1}$ alfaxalone and 3.6 $mg \cdot kg^{-1}$ alfadolone acetate). Anaesthesia and muscular paralysis were maintained by a continuous intravenous infusion that contained Althesin (3 $mg \cdot kg^{-1} \cdot h^{-1}$), Flaxedil (gallamine triethiodide, 15 $mg \cdot kg^{-1} \cdot h^{-1}$), supplemented with glucose and isotonic saline. Body temperature was kept at 38°C. Artificial respiration was maintained at 25 strokes per minute, and the volume of inhaled air was adjusted to maintain pCO_2 between 3.8 and 4.2%. The electrocardiogram was monitored throughout the experiment. The skull was cemented to metal bars rigidly fixed to the Horsley-Clarke frame, which enhanced recording stability. Small holes (2 mm diameter) were made in the skull above each hemisphere to give access to the region of area 17 corresponding to the representation of the area centralis (stereotaxic co-ordinates: L1-L2, P1-P3). A recording chamber was cemented on the cranial bone and filled with agar or high density mineral oil (Serva, 60000 cst) once the electrode had been positioned above the cortex through a small incision made in the dura. All surgical procedures were performed in conformity with national (JO 87-848) and European legislation (86/609/CEE) on animal experimentation.

Optical correction was assessed by retinoscopy (skiascopy) and by reflection of direct tapetal illumination on a stimulation screen (457 cm). Three-millimetre artificial pupils were used after retroprojection of the eye fundus. Visual stimulation was carried out using an in house, custom designed computer controlled visual stimulator developed by Gérard Sadoc (CNRS). Intracellular sharp electrode recordings were made using 60 to 80 M glass micropipettes filled with 2 M potassium methyl sulphate (KCH_3SO_4), 3 M potassium acetate (KAc), or 3 M potassium chloride (KCl) [5]. Impalement was usually achieved by concomitantly ringing the variable buzzer capacitor of the Axoclamp-2A and advancing the electrode tip by a step of 1–3 microns. A small retaining current (-0.1 to -0.2 nA) was applied during the first

few minutes and removed after stabilization of the resting membrane potential. The bridge was systematically balanced using a standard hyperpolarizing test pulse (100 ms, −0.2 to −0.5 nA). Patch-clamp whole cell recordings were obtained with low impedance (4–5 M) pipettes containing gluconate solution (140 mM potassium gluconate, 10 mM Hepes, 4 mM ATP, 2 mM $MgCl_2$, 0.4 mM GTP, 0.5 mM EGTA (KOH), with pH adjusted to 7.3 and the osmolarity adjusted to 285 mOsm). A tip offset potential of 10 mV was subtracted from the patch voltage records off-line. Voltage signals were low-pass filtered (with a cut-off frequency of 10 kHz) and stored on a video recorder or a DAT. On- and off-line data processing was done using a custom written software (Acquis1, Gérard Sadoc, ANVAR-Dipsi) and re-acquisition was typically made at 4 kHz feeding a 12 bit AD converter, after low-pass filtering (8 poles-Bessel) at half of the sampling frequency.

2.2. Psychophysics

The stimuli were displayed on a Sony Trinitron monitor (GDM-1601/1950) refreshed at 60 Hz with a spatial resolution of 1 280 × 1 024 pixels, 8 bits gamma corrected. A horizontal and a vertical Gabor patch (Gaussian-weighted sinusoids, contrast 40%, $\sigma = 0.5°$, 1.5 cycle per degree at 114 cm) were presented against a uniform grey background (50 $cd \cdot m^{-2}$). Apparent motion sequences were produced by displacing a Gabor patch between each frame. Different speeds were obtained by changing the jump size, with a fixed inter-frame interval (16.66 ms). Human observers viewed two apparent motion sequences separated by a 500-ms delay. One sequence contained a vertical Gabor patch collinear to the motion path (Collinear Sequence). The other sequence contained a horizontal Gabor patch orthogonal to the motion path (Parallel Sequence). In a 2-Interval Forced-Choice design, observers were simply asked to indicate which of the two sequences was fastest. The spatial displacement between frames was fixed in the collinear sequence (Reference Sequence), while it changed across trials in the parallel sequence (Comparison Sequences). To minimise the possibility that observers based their judgement on the duration or on the length of the motion trajectory, the number of frames was randomly varied from one interval to the next (range three to five frames for a total duration of 50 to 80 ms). The direction of motion, upward or downward, was chosen at random for each interval in each trial.

3. Results

Let us first summarize the current knowledge of cortical receptive fields based on the sole study of extracellular responses. Cortical cells, compared with retinal and to a lesser extent thalamic cells, have a low spontaneous activity level (below 1 $a.p. \cdot s^{-1}$), so that their receptive field is usually characterized by the excitatory discharge zone evoked by the ON- or OFF-transition of the visual stimulus. Numerous studies in the 70's have shown the existence of a 'silent' surround whose activation modulates the evoked response from a simultaneous stimulation of the discharge field [4, 23, 26]; review in [12]). What could be the anatomical substrate responsible of such centre-surround interactions? Primary visual cortical cells receive various sets of synaptic afferents. The first type of input, termed feedforward, respects the retinotopic organization and corresponds to the imprint made by the excitatory thalamic projection [20, 35]. The divergence of the terminal field of the geniculate axons is considered to be limited [18]. The gain of this initial cortical response is adjusted through inhibitory and excitatory intra-columnar cortical recurrent connections which still preserve at the cortical level the topographic neighbouring relationships defined at the retinal level [10]. A third set of afferents is conveyed through long-range intracortical 'horizontal' connections (review in [14]), and through feedback projections originating from higher cortical areas which connect cells whose respective RFs partially overlap [36]. The anatomical convergence of heterogeneous afferents onto a single cortical cell suggests that the extent of its functional integration field could vary according to the nature and the size of the afferent network recruited by the different configurations of stimuli (*figure 1*, adapted from [12]). The discharge field is derived from the combined action of the thalamic feedforward input (S-field, in green in *figure 1*) and the local intracortical circuits (in red, *figure 1*), but contextual modulation may be obtained by recruiting in addition the horizontal connectivity (in blue, *figure 1*). This latter part of the integration field is termed as subthreshold, since visual stimulation inside this field will not evoke per se spiking activity (D-Field in *figure 1*).

3.1. Electrophysiological study

For periods ranging from 30 to 615 min, 162 cortical cells were recorded intracellularly with sharp electrodes. The average resting membrane

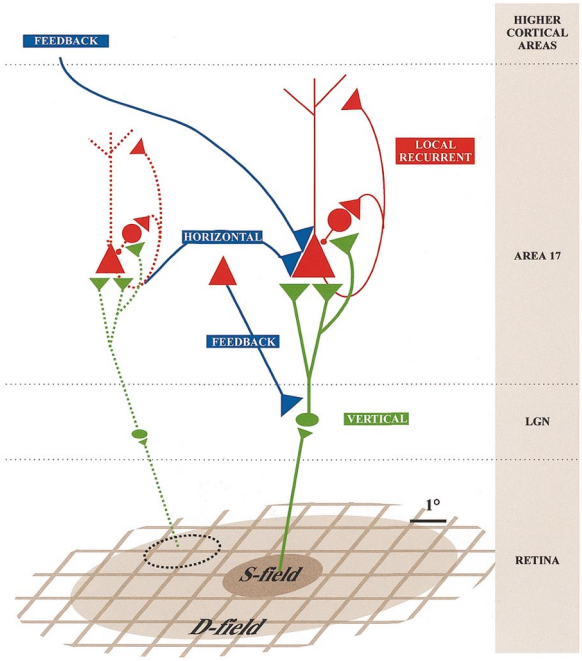

Figure 1. Subthreshold depolarizing field (D-field) and discharge field (S-field) in a primary visual cortical neurone. The discharge field is derived from the combined action of the thalamic feedforward input (green colour code) and the local intracortical circuits (in red), but contextual modulation may be obtained by recruiting in addition the horizontal connectivity (in blue).

potential was -66.1 mV (± 5.9 mV), input resistance between 10 and 70 MΩ, and spike height between 35 and 70 mV. In addition, twenty cells recorded using patch electrodes [7] were pooled with the sharp data base, leading to a total of 182 cells.

Responses to three types of visual stimulation were compared, each stimulus recruiting a different level of spatial and temporal summation. The simplest stimulus, 'sparse noise', was a contrast impulse [34], of small size ($<0.5°$) and duration (33–50 ms), of variable polarity (light or dark), and a random walk was used to visit all possible locations in the explored visual field for the two possible contrasts (light ON, dark OFF). The neural response to such stimuli can be considered as the 'impulse-response' and the resulting 2D-maps established for each contrast characterize the linear ON and OFF components of the spatial transfer function (*figure 2A1/B1/A3/B3*). Since cortical cells are best activated by correctly oriented stimuli [17], the second stimulus type consisted of contrasted bars with optimal orientation and length which were flashed in random positions across their width axis, in order to obtain a 1D-map of the receptive field (*figure 2C1/C3*). Finally, in order to optimize the synergetic activation of synaptic inputs, we also used compact (for the discharge field) and annular (for exploration of the surround) gratings whose orientation and spatial frequency were adjusted to optimize the evoked firing frequency (*figure 2D1*). Whatever the stimulus used and when the cell was initially at rest, significant depolarizing responses were evoked over regions much larger than the discharge field itself, unmasking in certain cells a very large responsive surround (D-field). For a given cell, the D-field size appeared to increase with spatial and temporal summation: on average, the equivalent diameter of the D-field was 2.5 times larger than that measured for the discharge field using sparse noise. This ratio increased to 3.3 for elongated bars and 5.6 for gratings.

Whatever the stimulation protocol used to map the receptive field, we observed that the intensity of the response (measured by the peak or integral value) decreases as a function of the test stimulus eccentricity relative to the centre of the discharge field (*figure 2B1/C1/D1*). In the case when a moderate depolarization of the membrane potential was imposed by an intracellular current, the size of the discharge field increased, recruiting part or the totality of the previously measured subthreshold D-field. The spatial extent of the synaptic integration field and its organization into a sensitivity gradient decreasing from the discharge field centre (*figure 2A1*) suggests that membrane potential fluctuations regulate the recruitment of inputs effective enough to trigger spike activity. This will generally be achieved by preserving the compact aspect of the responsive zone expressed at the spike level. More rarely, ectopic discharge regions can be revealed, sometimes as far as 10 degrees from the principal discharge zone measured at rest. The spatial extent of the discharge field, hidden by this 'iceberg' effect, can thus be considered as a dynamic variable dependent on the internal polarization state of the neurone and/or on the tonic synaptic bombardment by the rest of the network.

Moreover, we also demonstrated that subthreshold peripheral responses are orientation selective and, since orientation is not strongly expressed at the retinal or geniculate level, one can assume that they are most likely of cortical origin. The dependency of the time-courses of synaptic responses on the stimulus location relative to the discharge field centre suggests an indirect activation schema, consisting first of a serial retinotopic

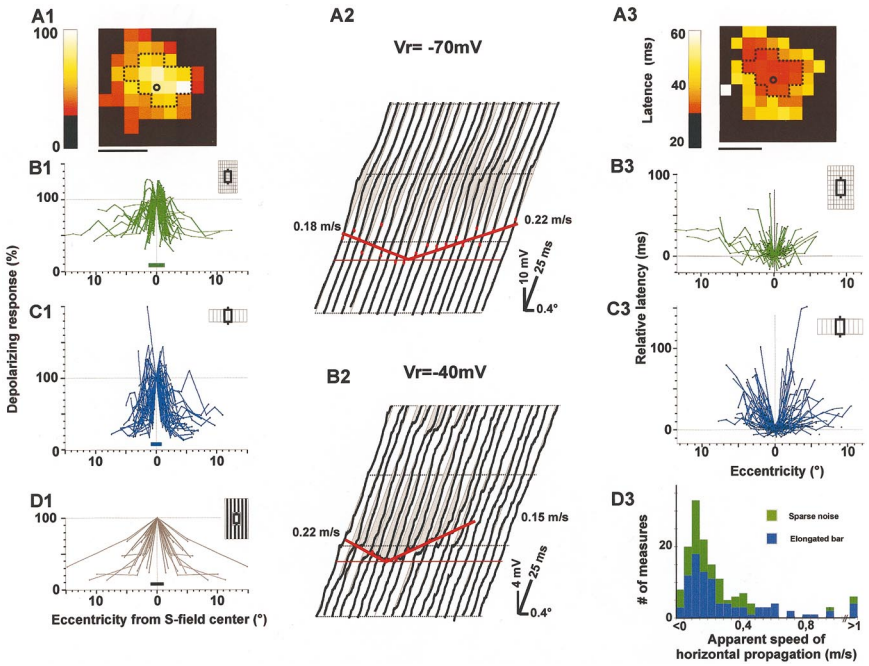

Figure 2. Spatial sensitivity profiles and latency basins of visually evoked synaptic responses. Left panel: **A1**: Colour coded map of the subthreshold response strength in a cortical neurone (D-field). The normalized intensity of the synaptic depolarization evoked in each pixel is colour-coded. The discharge field (S-field) is outlined by a dotted contour, and the dot indicates which pixel elicited the highest discharge rate. Horizontal scale bar, 2°. **B1-C1-D1**: The strength of the visually evoked depolarizing response is normalized relative to that observed at the location eliciting the maximal discharge (circle). Each individual profile represents for a given cell the change in response strength across the width or length of the RF, expressed as a function of the eccentricity of the test stimulus from the discharge field centre. These different profiles have been superimposed together on the same graph, each corresponding to a particular mapping protocol (**B1**, 2-D sparse noise ($n = 37$); **C1**, flashed bars ($n = 21$); **D1**, flashed ($n = 19$) or moving ($n = 2$) sinusoidal luminance gratings). The average discharge field extent is indicated by a thick horizontal segment. In the case of annular stimuli (**D1**), the abscissa corresponds to the distance between the centre of the S-field and the inner radius of the annulus. Central panel: **A2**: The waterfall representations illustrate the spatio-temporal profile of subthreshold depolarizing responses in a given cell at rest ($Vr = -70$ mV in **A2**) and in another cell during spike inactivation ($Vr = -40$ mV in **B2**, Section 2). The integral depolarizing and hyperpolarizing waveforms are indicated by shaded areas. Oblique lines indicate the best fit using a bi-linear regression accounting for the latency basin of synaptic responses. Similar AHSP values (0.15 to 0.22 $m{\cdot}s^{-1}$) are derived from the slope measurements (in red) in the X-T plane for both dominant excitatory (**A2**) and dominant inhibitory (**B2**) subthreshold responses. Right panel: **A3**: Colour-coded latency basin map of depolarizing responses evoked on the visual field. Black pixels indicate the absence of significant changes in the onset slope of the postsynaptic response The response latency is expressed as the absolute difference, in milliseconds, relative to the latency observed in the S-field centre (dot in **A1-3**). **B3-C3-D3**: Change in the latency of the subthreshold response expressed as a function of eccentricity relative to the S-field centre (abscissa in degrees of visual angle). Each cell is represented on a continuous graph, in response to sparse noise (**B3**) or to flashed bars (**C3**). Each latency basin is fitted by two linear regressions, and the slope of each fit, given in degrees per milliseconds in the visual field, is converted into m/s in the cortical layer plane (see text). The distributions of apparent speed of horizontal propagation (in $m{\cdot}s^{-1}$), established for each stimuli class, are shown in **D3**.

projection onto the cortex that will then be relayed to another distal cortical locus by the horizontal connectivity. Our results show that, independently of the method used (*figure 2*, sparse noise *B3*, elongated bars *C3*, gratings (not illustrated)), the evoked latency of the subthreshold responses increases linearly with the stimulus eccentricity relative to the centre of the discharge field (delay of 10 to 50 ms for 3–10 degrees of eccentricity, in *figure 2A2*). These latency increases are in agreement with the hypothesis of a spread of evoked action potentials travelling along intracortical axons across the cortical layer plane. We derived an estimate of the apparent speed of horizontal propagation by converting the distance separating two loci of stimulation in the visual field into the corresponding distance in the cortex between the focal zones of activation fired by the sole effect of the feedforward projection [37]. For this purpose, we used, for cat area 17, an average cortical magnification factor of 1 mm for 1 degrees in retinal space. Our results show that stimuli flashed in the 'silent' surround of a given recorded cell receptive field evoke subthreshold responses which are re-

layed with the same velocity by the horizontal intracortical network (given by the slope of the spatial latency basin in *figure 2B3–C3*).

The apparent speed of horizontal propagation (ASHP) deduced from our in vivo experiments, although varying among cells between 0.02 and 2 $m \cdot s^{-1}$, is in 75% of the cases lower than 0.4 $m \cdot s^{-1}$, i.e. the order of magnitude of conduction speeds measured in vitro and in vivo along non-myelinated horizontal axons [15, 27–29]. The value of the mode of the ASHP distribution remains at least one to two orders of magnitude lower than the conduction speeds reported for X- and Y-thalamo-cortical axons (8–40 $m \cdot s^{-1}$ [16]). Our latency analysis suggests that the information received at one point in the cortex through the serial feedforward afferents is then propagated radially by the horizontal connectivity to neighbouring regions of the visual cortex over a distance that may correspond to up to 10 degrees of visual angle. Primary visual cortical neurones would thus have the capacity to combine information issued from different points of the visual field, in a spatio-temporal reference frame centred on the discharge field itself. This ability imposes precise constraints in time and in space on the efficacy of the summation process of elementary synaptic responses.

The contextual influence originating from the 'silent' surround is not limited to the transmission of excitatory intracortical input. Similar analysis and detection methods have been applied to hyperpolarizing responses that were revealed when the membrane potential was artificially maintained at a depolarized level (-30 mV), away from the reversal potentials for chloride (-70 mV) and potassium (-90 mV) inhibitory synaptic currents. The goal of this protocol was to increase the visibility of subtractive inhibition by increasing the driving force of $GABA_A$ and $GABA_B$ currents and decreasing the AMPA/NMDA excitatory currents, and at the same time suppressing spike activity by inactivation of fast Na^+ conductances. This method leads to the same conclusion as for the excitatory events: a latency basin of hyperpolarizing events is observed, suggesting an intracortical propagation of inhibitory input with a velocity ranging between 0.1 to 0.3 $m \cdot s^{-1}$ (example in *figure 2B2*). The only difference with the spatial basin of latency observed for depolarizing responses is that the earliest onset inhibition following visual input is on average obtained for a point in visual space which is displaced by 1 to 2 degrees from the centre of the excitatory discharge field. Thus excitation and inhibition, although they may spatially overlap later in time, seem to take their origin in regions of the visual field which are spatially distinct. This result is reminiscent of extracellular observations made in layer VI cells in monkey V1 [24]. Our electrophysiological data also agree with the recent description of a horizontal connectivity network of interneurones that can extend over several millimetres in the cortical layer plane, thus exerting suppressive influences over a cortical distance corresponding to several degrees of visual angle in retinal space [21].

3.2. Psychophysical correlates

An obvious consequence of these observations is that cortical cells in area 17 of the cat analyse the visual scene over a window of spatial sensitivity much wider than the one predicted on the basis of the hierarchical convergence model [17]. The subthreshold receptive field extends far beyond the discharge field, thus enabling the cell to link distant information across the visual field (left panel, *figure 2*). If the average extent of the D-field is converted into a cortical distance, the value roughly corresponds to the maximal extent of the axonal horizontal projections of layer II-III or layer VI cortical cells (reviewed in [14]). Interestingly our measure of the synaptic integration field at the cortical level is within the same range as that reported by psychophysicists for the so-called perceptual 'association field', and thus may provide a cellular substrate for this psychophysical effect. Association fields, which have been extensively studied in humans, are usually defined by quantifying facilitatory or suppressive changes in the detectability of a central target when adding a contextual periphery [11, 32, 33, 38]. The largest interaction effects between the target and the lateral masks are found when the stimuli are oriented and co-aligned, suggesting that 'lateral' connectivity in visual cortex may participate in establishing such facilitation.

Our electrophysiological studies in the anaesthetized animal also indicate the existence of spatio-temporal constraints that could control the efficiency of synaptic summation. At a given cortical locus, the temporal summation of activity evoked by several visual stimuli presented in different retinal loci should differ, whether these are flashed simultaneously or sequentially with short interstimulus temporal intervals. In other words, we predict at the level of V1 cells that spatio-temporal sequences where the 'silent' periphery of discharge

field would be stimulated some tens of milliseconds before the presentation of a stimulus in the discharge field (centripetal surround → centre sequence) should result in a phase equalization of the onset of synaptic events independently of their spatial origin (*figure 3*). The resulting evoked activity should then be larger than that induced by a simultaneous presentation or with a centrifugal sequence (from the centre to the surround) of the same test stimuli.

Those predictions inspired a series of psychophysical studies, whose preliminary results strongly support the following working hypothesis: the temporal characteristics in the recruitment of the 'horizontal' intracortical connectivity could affect the perception of apparent motion [25]. The 'Phi' or apparent motion is an illusory percept, classically described when the same target is repeatedly flashed at different moments in time in different positions of the visual field ordered along an imaginary trajectory. Although at each moment in time the observer only sees a static image at a given position of the visual field, he actually reports the perception of the spatio-temporal sequence as a continuous motion along the trajectory (or 'association pathway' *figure 3*). The percept is conditioned by the complexity of the test stimulus (form and structure), the time of presentation, the interstimulus interval and spatial separation [1].

In collaboration with Sebastien Georges and Peggy Series, we tried to determine possible perceptual biases evoked by the stroboscopic presentation of a test stimulus chosen to selectively activate primary visual cortical neurones. For this purpose, we used Gabor patches, namely oriented sinusoidal luminance gratings whose modulation is weighted by a bi-dimensional Gaussian function. The form, the spatial frequency and the anisotropy along the main orientation axis precisely reproduce the spatial sensitivity profiles of cortical discharge fields [8, 19]. Our results show that the apparent speed of motion induced by a sequential presentation of Gabor patches in different positions of the visual field was estimated faster by the subject when the orientation of each Gabor patch was collinear to the axial direction linking the different positions than when they were orthogonal to the 'association' pathway. This effect, summarized in *figure 4*, may be quantified by the ratio between the speed of the comparison 'parallel' sequence over that of the 'reference' collinear sequence for which the subject reports equality in speed. The perceptual bias can be as strong as 3-fold, and its strength explains why observers find in more than 80–95% of cases that 'parallel' sequences are faster than 'horizontal' even if both composite stimuli have the same physical speed. The physical reference speed for which the effect is maximal corresponds to $64°\cdot s^{-1}$ in the visual field, which would be equivalent for parafoveal tests to an apparent ASHP propagation speed of $0.2\ m\cdot s^{-1}$ in man V1 cortex. Remarkably, and as predicted, this value extrapolated in human cortex is well within the range of those we measured electrophysiologically in cat area 17.

This type of unexpected psychophysical effect is also reminiscent of the model introduced by Field and coworkers [11], who proposed that the local stimulation by an oriented edge in one location induces facilitation along an association trajectory which is collinear with the orientation axis of the inducer. In addition a certain number of proper-

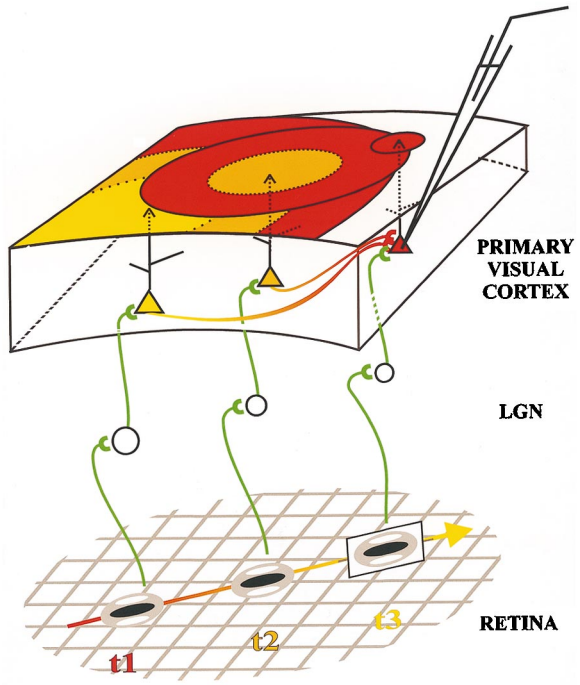

Figure 3. This cartoon depicts the intracortical propagating waves of visually evoked spiking activity triggered by the sequential presentation of three Gabor patches on the retina. The respective orientations of those three stimuli are co-aligned with the motion axis of the 'association pathway'. The presentations of the Gabor patches are done sequentially (t1 then t2 then t3), and the interstimulus interval (ISI = t3–t2 = t2–t1) is adjusted so that the serial retino-thalamo-cortical feedforward input reaching the intracellularly recorded cell (red triangle) rides in phase the evoked 'horizontal' intracortical waves. The position of the 'horizontal' activity wave as a function of the time elapsed from the presentation of the first stimulus (t1) is colour-coded.

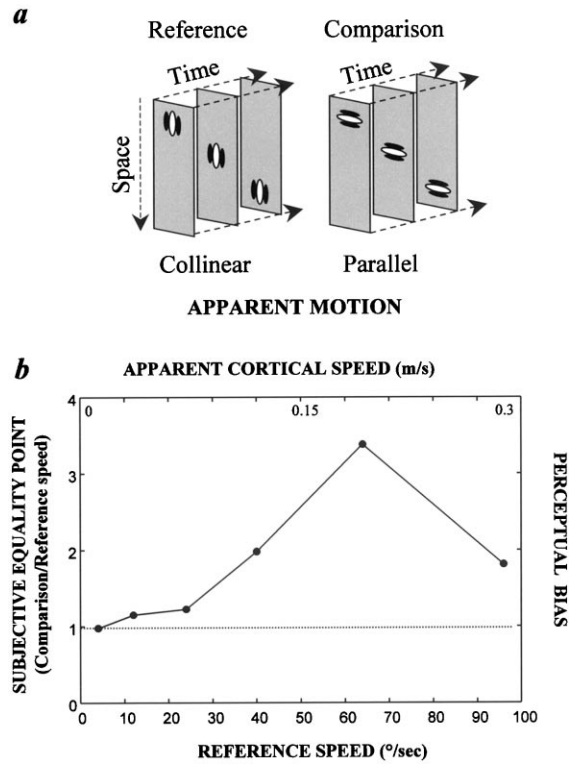

Figure 4. (**a**) Space-time plots of the apparent motion sequences. A trial consisted of the successive presentation of two short apparent motion sequences of a vertical (left cartoon, reference Collinear Sequence) and a horizontal (right cartoon, comparison Parallel Sequence) Gabor patch moving along a vertical axis. In a 2-Interval Forced-Choice design, observers indicated which sequence appeared faster. (**b**) The speed of the parallel sequence eliciting a subjective equality (50% probability) in choice when compared with the reference sequence was measured for six different reference speed values, ranging from 4 to 96°·s^{-1}. The ratio of both speeds (comparison/reference) quantifies the perceptual bias experienced for collinear contours. This effect peaks for an absolute reference speed of 64°·s^{-1}, corresponding to an apparent intracortical 'horizontal' speed of 0.2 m·s^{-1}.

ties, not predicted by Field et al.'s model, could simply arise from the spatio-temporal constraints in the intracortical synaptic integration that we previously presented. As predicted when using a retinocortical magnification factor appropriate for foveal vision in humans (3 mm per degree), the amplitude of the perceptual bias in detecting apparent motion becomes maximal when the physical speed of the apparent motion corresponds in the visual field (0.06°·ms^{-1}) to the speed of the propagating wave of horizontal intracortical activity (0.2 m·s^{-1}). In other words, the percept of speed (subjective evaluation of the intensity of the motion signal) would be over-estimated when the feedforward activation produced by the spatio-temporal sequence of Gabor patches arrives in phase at any point in cortical space with the horizontally propagated information already spread by the stimuli that were previously flashed in sequence.

We predict that this condition of temporal synchronization between thalamic feedforward and intracortical horizontal inputs amplifies and even speeds up the excitatory message relayed by the primary visual cortex to cortical centres specialized in motion detection (MT, [39]), resulting in an over-estimation of the absolute speed of the apparent motion. The strong dependencies that were found on physical attributes of the stimulus such as (i) the speed range for which the functional expression of the perceptual bias is favoured, (ii) its aspect ratio anisotropy, (iii) its orientation angle relative to the 'association' axis, all suggest that this perceptual bias reflects the anatomofunctional constraints imposed by the conduction velocity and geometry of intracortical axons. The functional preference revealed by psychophysical methods can be viewed as a resonance between the physical characteristics of the stimulation and the spatio-temporal bandwidth of the horizontal network, with the help of which cortical neurones remain capable of binding events originating at different times and locations in the visual space. In other words, the limitation in the conduction speed of horizontal axons would affect in an unexpected way our perceptual capacity to extract motion information from a succession of static snapshots stolen from our visual environment.

Acknowledgements

This work was supported by funding from CNRS, Foundation Fouassier and grants from INSERM (Progres 100-954), GIS Cognisciences and the Human Frontier Science Programme (RG 0103/1998B). One of the authors, Vincent Bringuier, passsed away recently and we dedicate the present work to his memory. We thank Dr Kirsty Grant for helpful comments on an earlier version of the manuscript and help with the English.

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