1. **Horizontal connectivity in V1 : Prediction of coherence in contour and motion integration**

2.

3. Abbreviated Title : Horizontal propagation of “network belief” in V1

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18. Abstract

19. This study demonstrates the functional importance of the Surround context relayed laterally in V1 by
20. the horizontal connectivity, in controlling the latency and the gain of the cortical response to the
21. feedforward visual drive. We report here four main findings : 1) a centripetal apparent motion
22. sequence results in a shortening of the spiking latency of V1 cells, when the orientation of the
23. local inducer and the global motion axis are both co-aligned with the RF orientation preference; 2) this
24. contextual effects grows with visual flow speed, peaking at 150-250°/s until matching the propagation
25. speed of horizontal connectivity (0.15-0.25 mm/ms); 3) For this speed range, axial sensitivity of V1
26. cells is tilted by 90° to become co-aligned with the orientation preference axis; 4) the modulation
27. strength by the surround context correlates with the spatiotemporal coherence of the apparent
28. motion flow. Our results suggest an internally-generated binding process, linking local (orientation
29. /position) and global (motion/direction) features as early as V1. This long-range diffusion process
30. constitutes a plausible substrate in V1 of the human psychophysical bias in speed estimate for
31. collinear motion. Since demonstrated in the anesthetized cat, this novel form of contextual control of
32. the cortical transfer function is a built-in property in V1, whose expression does not require behavioral
33. attention and top-down control from higher cortical areas. We propose that horizontal connectivity
34. participates to the propagation of an internal “prediction” wave, linking contour co-alignment and
35. global axial motion at an apparent speed in the range of saccadic-like eye-movements.
36.

37. Introduction

38. Low-level visual perception is often described as a “pop-out” holistic process, elevated at the
 39. state of “consciousness”, independently of behaviorally directed attention. At the perceptual level,
 40. Gestalt rules link stimuli according to feature similarity, spatial proximity or common fate (1, 2). Their
 41. neural implementation is thought to occur at various stages of visual cortical processing (3) and best
 42. captured, in terms of receptive field (RF) computation, as the combination of a smooth spatial
 43. “association field” operator in space (4, 5), and a diffusion kernel in time (6). However, the detailed
 44. synaptic implementation and the cortical regionalization of this dual space-time mechanism remain
 45. largely unknown (review in (7)). An unsolved issue, which is central to this study, is to determine to
 46. which degree “horizontal” connections, intrinsic to the primary visual cortex (V1), are instrumental to
 47. the neural implementation of Gestalt laws.

48. Classically, the consensus is that binding in space and time are processed in separate cortical
 49. areas, respectively in V1 for local attributes of form and contour integration, and in MT for global
 50. motion (8-10). Although the functional expression of contour-related responses in V1 has been shown
 51. to depend on the behavioral attention context and to be task-specific (11), it requires the triggering of
 52. a stimulus-driven bottom-up process already detectable in the anesthetized brain (12-14). Local
 53. circuits, intrinsic to primary visual cortex such as the long-range horizontal connections, are involved in
 54. contour integration, but the final binding process is gated and tuned in strength by selective top-down
 55. signals conveyed by re-entrant cortico-cortical pathways ((11, 15); review in (16)). In contrast, in terms
 56. of hypothetical cortical circuitry contribution, neural correlates of motion binding appear well
 57. established in MT (17-19) but far less documented in V1 (but see (20)).

58. In spite of many intracellular receptive field (RF) studies in cat V1 (21-24), only a few have directly
 59. measured the synaptic nature of contextual influence originating from the “silent surround” (25-30). A
 60. striking feature from our own observations is that the strength of distal synaptic echoes exponentially
 61. decreases, while their latency linearly increases, with the relative eccentricity of the stimulus from the

62. RF center. If intracellular studies quantify synaptic convergence of lateral input, optical imaging, in a
63. converse way, monitors the full network depolarization pattern and dynamics in response to a local
64. stimulus. Intrinsic imaging reveals the spatial extent of the diffusive pattern of intracortical activity,
65. spread across several hypercolumns (up to 6° in cat, in (31)). Mesoscopic dynamic imaging, using
66. voltage sensitive dyes with a temporal activation precision in the ms range, report depolarizing front
67. waves propagating across the superficial layers of V1, observed both in the ongoing and visually driven
68. states (*non human primate (NHP)* (32-36); *cat* (37-40); *rat* (41)). Their speed range is comparable
69. across mammalian species and matches remarkably that inferred from our intracellular recordings in
70. the cat (between 0.05 to 0.50 mm/ms in (26)).

71. Intracellular recordings provide a unique way to dissect out the diversity of synaptic input
72. connectivity pattern across individual V1 cells and, at the same time, infer, through selective
73. averaging, the mean functional kernels of feedforward and lateral synaptic inputs composing the V1
74. receptive field. A prior study in our lab (29) proposed a new feature-specific averaging method, while
75. keeping the mapping stimulus geometry invariant, across cells, in a receptive-field-centric framework.
76. This was done by realigning each of the individual subthreshold maps relatively to a common origin
77. and “0°” reference axis, corresponding respectively to the center and the preferred
78. orientation/direction of each recorded RF. The averaging of 25 cells demonstrated that, irrespectively
79. of single cell RF diversity, the mean synaptic connectivity kernel of V1 neurons receives predominantly
80. iso-oriented inputs from neighboring collinear V1 hypercolumns, and that its spatial organization
81. pattern exactly mirrors the perceptual “Association Field” for collinear contours in human
82. psychophysics (4, 42).

83. The extensive intracellular study on dynamic Center-Surround interaction we present here - on a
84. larger cell sample (n=65) - is based on the same premise. It searches to maximize the paired neighbor-
85. to-neighbor interactions between Surround and Center and quantify a novel form of contextual
86. control on the spiking responsiveness of V1 cells. For this purpose, we have designed here a variety of
87. multi-stroke apparent motion (AM) sequences of specific speed and spatial anisotropy, which, under

precise timing and local feature co-alignment conditions, allowed us to control the temporal phase between horizontal and feedforward inputs. Two sets of visual protocols were applied separately in two distinct sets of cells with complementary objectives. The “**cardinal**” protocol (Fig. 1B), was designed to : i) optimize the visibility of synaptic inputs originating laterally from the “Near” RF surround, outside the spiking “minimal discharge field” (MDF), but potentially overlapping with the subthreshold depolarizing receptive field (SRF)); ii) probe for a possible axial bias in the preferred recruitment of contextual Surround information integration, using 2-3 stroke AM sequences along the two main (length/width) axis of the RF). The second series of protocols, termed “**radial**” (Fig. 1C), was based on a more conservative definition of the synaptic feedforward cortical imprint, no longer defined only by its spiking discharge field (MDF) but including as well the surrounding depolarizing SRF. This additional requirement limited the Surround stimulation to “Far” regions outside the SRF only. It was meant to minimize the risk of spurious feedforward contamination when probing the location the closest to the RF borders (position D1 in Fig. 1A). To compensate for potentially weaker Surround responses, we increased the number of AM strokes and imposed radial symmetry in order to recruit simultaneously more sources in the RF periphery at the same relative Surround eccentricity.

Fig 1. Working Hypothesis and Visual Stimulation Protocols

[A] : Working Hypothesis : the AM sequence is designed such as to synchronize the synaptic activation time of horizontal volleys, evoked by the sequential presentation of 2 to 5 Gabor patches (GP) in the Surround, with the feedforward activation of the RF Center (shaded rectangle in the D0 position). The Surround GPs, regularly spaced from “Far” (D5) to “Near” (D1) periphery along the apparent motion path (horizontal axis), are flashed in succession at high contrast. The test reference GP, terminating the AM sequence, is flashed at low/high contrast in the RF center. Each orange arrow represents the lateral propagation of the presynaptic volley elicited by each distal GP. Other synaptic recruitment paths potentially contribute also to Surround-Center modulation, in particular cascades of proximal neighbor-to-neighbor links (grey arrows).

[B] “Cardinal” Protocol : the two columns illustrate the exploration of the two cardinal axis (horizontal for the RF orientation preference; vertical for the RF width axis) with 2 or 3-stroke AM sequences of iso-oriented stimuli

115. (“collinear”, first row; “parallel”, second row) or cross-oriented stimuli (two bottom rows, same motion paths
116. but the local inducer is now orthogonal to the RF orientation preference).
117. **[C]: “Radial” Protocol** : the two columns illustrate the various AM flow patterns (individual rows), either
118. funneled along a given motion axis (**SECTOR**, left), radially contracting (CP: centripetal) or expanding (CF:
119. centrifugal), or across the full Surround (**FULL**, right). In the SECTOR condition, two opposite motion axes are
120. symmetrically explored, either aligned with the RF orientation preference (horizontal axis ($\pm 30^\circ$) in rows 1, 2 and
121. 4) or its width axis (vertical axis ($\pm 30^\circ$), row 3). In the FULL condition, all directional motion axes (discretized by
122. 30° steps) are stimulated concomitantly and intersect the RF center (horizontal grey icon). From top to bottom,
123. each row illustrates one specific configuration of AM flow: 1) centripetal collinear flow (**CP-ISO**) from Surround to
124. Center (red, row 1); 2) centrifugal collinear flow (**CF-ISO**) from Center to Surround (green, row 2), 3) centripetal
125. cross-oriented flow (**CP-CROSS**) across the RF width axis (gold, row 3); 4) randomized collinear pattern (**RND-ISO**)
126. where each successive GP location has been randomized in space and time (blue, bottom row). Note that in all
127. the conditions other than CF-ISO, the last GP of the sequence is flashed in the RF center. See [Text](#) for details.
128. -----

129. The “working hypothesis” we tested posits that the spatio-temporal optimization of the cortical
130. responsiveness control should be reached, where, in space, the local orientation of each Surround GP
131. matches that of the recorded RF (as expected from the “Association Field” profile), and when, in time,
132. the phase of the stimulation of each surround node compensates for the lag of the postsynaptic
133. response, due to the dependency of the PSP latency on the eccentricity relative to the RF center
134. (Fig. 1A, “latency basin” in Fig. 2A). Our functional prediction is that a latency shortening and an
135. overall cortical gain amplification of the composite PSP produced by the AM sequence invading the RF
136. center should be observed when the global flow speed is adjusted to merge in synchrony the
137. respective synaptic impacts of the lateral and feedforward drives onto the intracellularly recorded cell.

138. This study addresses the importance of the Surround context dynamics relayed laterally in V1 by
139. the horizontal connectivity, in controlling the timing and the responsiveness gain of the cortical
140. response. It also gives evidence for neural correlates of “filling-in” responses at the earliest stage of
141. visual cortical processing, i.e. the primary visual cortex. Remarkably, these responses are shown to be

142. specific of co-alignment, and their timing anticipates the occurrence of the same orientation feature
143. (“expected” in Bayesian terms) in the RF center, even in the absence of feedforward activation. We
144. infer, from a detailed contextual synaptic interaction analysis, a conceptual framework which accounts
145. for the neural correlates in V1 of specific Gestalt-like visual configurations, linking local (orientation)
146. and global (contour integration, motion) features.
- 147.

148. **Material and Methods**

149. **1. Animal preparation and electrophysiological recordings**

150. All experiments were performed in anesthetized (alfaxalone, Alfaxan®, 2.5 mg/kg/hr) and
 151. paralyzed (pancuronium Pavulon® (0.1 ml/kg/hr) or rocuronium Esmeron®, 4 mg/kg/hr) adult cats of
 152. either sex, in accordance with the American Physiological Society’s Guiding Principles for the Care and
 153. Use of animals. Animals were bred in the Central CNRS Animal Care Facilities under veterinary and
 154. National Ethical Committee supervision (MESR agreement: n°201603111-3088501). Anesthesia depth,
 155. analgesia level and the general physiological state stability were continuously monitored from the
 156. recording and analysis of EKG and extradural ECoG signals. End-tidal CO₂ was maintained between 3.5
 157. and 4.5%, and body temperature was regulated around 38°C throughout the experiment. Once the
 158. animal’s head was fixed to the stereotaxic frame, and the craniotomy performed, we checked again
 159. the presence of a slit pupillary state, indicative of adequate anesthesia during the surgery phase. Then,
 160. atropine (1%) and phenylephrine (5%) were applied to both eyes to dilate pupils, block the
 161. accommodation and withdraw nictitating membranes, while artificial pupils and corrective lenses
 162. were used to protect the eyes and focus the backprojection of the eye fundus on the stimulation
 163. screen.

164. *In vivo* intracellular recordings of cortical cells were performed in the primary visual cortex (area
 165. 17) using sharp Glass electrodes pulled from 1.5-mm-thick borosilicate capillaries (World Precision
 166. Instruments Inc.). Electrodes were filled with a 2M potassium methyl sulfate (pH ranging from 7.2 to
 167. 7.4), 4 mM KCl solution for compensating the tip potential, and 1.5% biocytin. Electrode resistances
 168. before impalement ranged between 70 and 130 MΩ. Cells were recorded in current clamp bridge
 169. mode using an Axoclamp 2A (Axon Instrument inc.) or a SEC-05X (NPI inc.). The average resting
 170. potential was between -62 to -78 mV (mean $\pm$ σ = -66,8 $\pm$ 8,3 mV) with no or a slight holding current
 171. ($\leq$ -0.5 nA) when needed. Signals were filtered and amplified with a CyberAmp380 (Axon Instrument
 172. inc.) and digitized at 10 kHz by an ITC-1600 (InstruTECH®) card. Based on recording depth and the

173. laminar location and morphological identification of fourteen biocytin labeled cells, the overall
174. sampling was distributed from supra- to infra-granular layers. However, in view of the limited number
175. of labelled cells (experimentally constrained by gliolysis increase with the length of recording) and a
176. slight bias for recordings in deep layers, no laminar study was done in this reduced sample.

177.

178. **2. Visual stimulation**

179. Visual stimuli were generated, using the ELPHY home-made software (G. Sadoc, UNIC-CNRS), on a
180. CRT P31 green monochrome monitor positioned at 57 cm ($1\text{ cm} = 1^\circ$ of visual angle) at refresh rate of
181. 60 Hz (19 inches, 640 x 480 pixels) for the “cardinal” protocols, and on a gamma-corrected LCD green
182. monitor at 28.5 cm from the cat’s retinal plan ($0.5\text{ cm} = 1^\circ$ of visual angle) at a refresh rate of 144 Hz
183. (27 inches screen, 1920 x 1080 pixels) for the “radial” protocols.

184. **2.1. Initial quantification of RF optimal features :**

185. The receptive field (RF) position of each recorded neuron and its ocular dominance were initially
186. established using moving light bars. Stimulation was done through the dominant eye for the rest of the
187. experiment. Subthreshold ON and OFF (SRF) sub-regions and spike minimal discharge fields (MDF)
188. were then mapped by forward correlation of visual responses to a random “sparse noise” (SN)
189. protocol where white (40 cd/m^2) and dark (1 cd/m^2) non-overlapping squares were presented one at a
190. time for 16-34 ms against a grey background (20 cd/m^2) in each position of the exploration grid (8x8 or
191. 20x20 pixels) centered over the coarse RF region. In some cells, an additional 1D mapping was done
192. with an optimally oriented thin long bar flashed randomly at various eccentricities across the RF
193. width (Fig. 2A).

194. Once the RF location defined, the preferred orientation, phase and spatial frequency of the cell
195. were determined using a dense Gabor Noise (GN) stimulation protocol (43), in which flashed (16-34
196. ms) Gabor patches (GPs, adjusted in size to the s-DF extent) were randomly presented at six different
197. orientations (with 30° steps), four phases (0° , 90° , 180° and 270°) and five spatial periods (ranging

198. from 0.1 to 4.9 cycles per degree of visual angle). For each cell, the parameters of the Gabor patch
 199. eliciting the strongest response in the RF center were retained to compose a template of preferred
 200. features of the inducer (independently of its position) in the subsequent apparent motion (AM)
 201. sequences. In order to evoke a sizeable synaptic “horizontal” response, the GP flashed in the Surround
 202. were always presented at high contrast ($\text{mean} \pm \sigma = 92.5 \pm 11.5 \%$; range 75-100%), whereas the
 203. feedforward central stimulus was flashed in the MDF either at low or medium contrast ($\text{mean} \pm$
 204. $\sigma = 40.6 \pm 24.5 \%$; range (25-100%)).

205. 2.2. “Cardinal” Apparent Motion (AM) Protocol :

206. In order to assess the dependency of the center-surround interaction on local orientation and
 207. global motion, we first designed three-stroke center-surround AM protocols for which the Gabor
 208. patches were flashed along the two “cardinal” RF axes defined by the RF preferred orientation and
 209. width (Fig. 1B). We looked at the modulatory effect that a two-stroke activation of the “silent”
 210. surround would produce (along each of these axis) on the response to a test stimulus flashed within
 211. the MDF (the third stroke). Randomly interleaved three-stroke stimulation sequences were applied
 212. moving away from the receptive field center (“centrifugal” (CF) condition, green arrows in Fig. 1B), or
 213. from the surround to the center (“centripetal” (CP) condition, red arrows) from one side of the RF at a
 214. time.

215. The size of the Gabor patch mask was set at 150% of the length of the spiking discharge field
 216. while the standard deviation of its Gaussian envelope was set at 20%. The stimulus inter-node distance
 217. was of 120% of its length, often leading the more proximal GP to partially encroach on the border of
 218. the impulse SRF. The orientation of the local inducer could be defined two ways, either in relation with
 219. the RF orientation preference, or in relation with the AM motion axis. These two analysis contexts will
 220. be considered separately in the Results. Here, by sake of uniformity with the “radial” protocol, the
 221. ISO- and CROSS- conditions are defined relative to the chosen AM axis. The complete set of 16
 222. Surround-Only stimulations (Fig. 1B, left column) included 8 conditions [CP-ISO_main-axis, CP-
 223. ISO_width-axis, CP-CROSS_main-axis, CP-CROSS_width-axis, CF-ISO_main-axis, CF-ISO_width-axis, CF-

224. CROSS_main axis, CF-CROSS_width axis] X 2 direction conditions (one side at a time)], to which 2
 225. control conditions (1 Center-Only + 1 Blank trial, where no stimulus was presented) were added.
 226. Hence a total of 18 conditions was completed in 13 cells. Center-Surround interactions were tested in
 227. 23 cells with full AM sequences terminating in the RF center (Fig. 1B, right column), under 10
 228. conditions [4 conditions (CP-ISO_main-axis, CP-CROSS_width-axis, CF-ISO_main-axis, CF-CROSS_width-
 229. axis) X 2 directions (one side at a time) + Center-Only stimulation + 1 blank]. For each study
 230. (Surround-Only; Surround-Center), the different stimulus conditions were interleaved randomly in
 231. each trial block. Recordings lasted for 20 blocks.

232. Given the constraint of the monitor distance (57 cms), its refreshing rate (60 Hz), and the fixed
 233. duration of the static Gabor inducer presentation (16 ms), individual cell AM speed values only
 234. depended on the size of the recorded RF which was used to define the sequential interstimulus step
 235. distance. Accordingly, AM speeds were preset in the suitable range of values to compensate for the
 236. dependency of visual PSP latency with relative eccentricity (26, 29).

237. **2.3. “Radial” Apparent Motion (AM) Protocol :**

238. This series of protocols was done with a larger (27 inches) and faster screen (144 Hz), using a
 239. shortened viewing distance (28.5 cms), which allowed a more extensive exploration of the “Far”
 240. surround. The visual field was paved with a grid composed of 5 concentric rings of increasing
 241. eccentricity centered on the RF covering up to 25° in the surround (Fig. 1C). To the difference of the
 242. “cardinal” protocol, where stimulus size and spacing were defined relatively to the spiking MDF size,
 243. the distance between each outer ring and the patch size were adjusted in this new protocol to the full
 244. extent of the subthreshold depolarizing receptive field (SRF) mapped with impulse stimuli. This change
 245. in the RF core definition, from that used in the “cardinal” protocol condition, was done to prevent, on
 246. a cell-by-cell basis, a direct feedforward contamination by the stimulation of the most proximal
 247. Surround location (position D1 in Fig. 1A).

248. Additionally, in the “radial” protocol, we designed Apparent Motion sequences whose spatio-

temporal coherence was parametrized to dissect the dependency of the inducer orientation relative to the motion path, as well as the spatio-temporal congruency within the AM flow (see Results). For each recorded cell, the reference AM sequence was the centripetal iso-oriented configuration (CP-ISO, top “red” row in Fig. 1C), where the local inducer orientation was either co-aligned along the preferred orientation axis of the recorded RF (SECTOR configuration, left column in panel 1C) or along the global motion axes (FULL configuration, right column). Three supplementary visual AM configurations were tested, in which the spatio-temporal structure of the local Gabor patch (GP, local inducer) sequence was altered, while keeping the overall stimulus energy distribution unchanged: i) in the first control condition, namely the centrifugal iso-oriented AM sequence (CF-ISO, second “green” row from the top, Fig. 1C), the temporal order of the sequential presentation of the co-aligned GPs was reversed, resulting in a centrifugal (CF) flow from Center to “Far” Surround locations; ii) the second control was designed to study the contextual impact of the local GP orientation relative to the motion axis. In the centripetal cross-oriented AM condition, the local orientation of the inducer was orthogonal to the motion axis (CP-CROSS, third “yellow” row from the top, Fig. 1C); iii) in the third control condition, the same retinal space (SECTOR or FULL) as in the CP-ISO condition of interest was stimulated with the same GPs (i.e., with the same number, features, and energy distribution at each step of the AM) but the coherence of the flows was randomized both in space and time (RND-ISO, bottom “blue” row). For each block, each stimulus location was visited only once, and the last stimulus location was the RF center. The repeated sequences were identical across blocks (pseudo-randomization).

The stimulus set in the “radial” protocol - where all contextual conditions were explored - was composed of 16 dynamic apparent motion sequences (4 conditions (CP-ISO, CF-ISO, CP-CROSS, RND-ISO) X 2 trajectories (with or without Center stimulation) X 2 configurations (SECTOR and FULL), and 21 stimulation types where Gabor Patches were flashed in isolation (5 peripheral locations X 2 conditions X 2 configurations + 1 GP flashed in the Center). In each block of trials, each stimulus was presented only once. Additionally, 6 “blank” trials were also included in each block. The resulting set of 43 stimulations was presented in random order in each block. Recordings lasted for 19-50 blocks (median

275. 50).

276. In order to optimize synaptic summation between Surround and Center stimulation, the AM
277. sequence speed was function of the spatial extent of the SRF and of the stroke duration of Gabor
278. patches and adjusted cell-by-cell in order to fit the latency basin of “Far” surround response latencies.
279. In the “radial” protocol where AM speed and stroke duration could be independently parametrized,
280. the stroke duration was in the 30 ms range (± 9 ms). It was 16.6 ms in the “cardinal” protocol.
281.

282. **3. Intracellular Data analysis**

283. **3.1. Data formatting :**

284. Spikes were threshold-detected in the raw traces and replaced by alpha functions in the membrane
285. potential (Vm) traces ($\alpha(t)=a*t*\exp(-t/\tau)$), where a is the slope at the peak of the second derivative of
286. the rising phase, and τ is the half-width of the spike), as done in previous studies (29). Resulting traces
287. were band-pass filtered (0.1-300 Hz) and peristimulus triggered waveform (PSTW) were averaged
288. across trials and conditions. Prior to any statistical analysis, all traces were down-sampled to 1 kHz and
289. smoothed using a sliding average window of 7 ms. For spikes, individual peristimulus time histograms
290. were smoothed using a Gaussian window ($\sigma= 3$ ms). For a given trial block containing all conditions,
291. the corresponding mean activity (average Vm and Spiking discharge rate) was subtracted from the raw
292. PSTWs and PSTHs.

293. **3.2. Response quantification and statistical significance :**

294. For the “cardinal” protocol, Z-test statistics (one tailed $p<0.05$) were applied to mean population
295. integral response values of the subthreshold response waveforms (dominantly depolarizing) compared
296. to resting state fluctuations. For the “radial” protocol, since a larger spectrum of stimulus conditions
297. was used, more extensive statistical analyses were done on the individual cell’s responses, without or
298. with selection criteria. All significance tests fell into two categories: quantifying the significance of a
299. response to a stimulus or comparing data statistics between two conditions. To do the former, we

300. relied on the activity during blank trials, which provides the null distribution for visual responses (i.e.,
301. the activity that would occur should the cell not respond to the stimulus, which was our “null”
302. hypothesis). Consequently, for each cell, the average ongoing synaptic or spiking activity recorded
303. during “blank” trials was subtracted from each evoked PSTW/PSTH trial activity. For the latter, we
304. used cell-by-cell paired comparison between distinct tested conditions. Statistical analysis was then
305. done using a randomization permutation test with 10^4 repetitions. In the remaining fifteen “non-
306. spiking” cells, analysis was restricted to subthreshold activity.

307. From these computations, we extracted the null hypothesis waveform envelope for a given
308. confidence interval at each point in time. Only cells with a response to the Center-Only condition
309. significantly larger than the blank ($p < 0.01$) in the interval 0-to-120 ms (“0” being the onset of the last
310. stimulation in the center when the RF was actually stimulated, “120”ms integrating most of the
311. feedforward onset and offset responses) were considered for further analysis. For PSTW and PSTHs,
312. respectively thirty-seven and twenty-two cells were retained after this verification and constitute the
313. population used for the Results section for the “radial” protocol.

314. **3.3. Quantification of the contextual change in response gain and phase:**

315. We quantified the time-course and the strength of the contextual control of the cortical transfer
316. function by measuring the changes in i) subthreshold latency and ii) the integral value of the
317. depolarizing postsynaptic potential (PSP) response to the complete AM sequence terminating in the
318. recorded cell’s receptive field. For the “cardinal” protocol, the latency measure was defined by the
319. onset of the mean PSP reaching significance (Z-test, $p < 0.05$). For the “radial” protocol, we chose to use
320. a more conservative measure to avoid spurious detections of fluctuations in the ongoing synaptic
321. noise. Accordingly, the latency change (Δ latency) was measured at half-height of the Center-Only
322. response amplitude peak, separately for Vm and spikes. For the response gain (Δ response), we
323. measured the change in the PSP depolarizing envelope integral (and, eventually, spiking integral),
324. relative to the Center-Only response, over the whole time-course of the test-response. Here, the
325. rationale was to integrate differences in evoked responses for all possible time relationships between

326. feedforward and lateral input. The same statistical analysis (randomization test, 10^4 repetitions;
327. $p < 0.05$) was repeated for PSTWs and PSTHs for both criteria. The paired-analysis was replicated across
328. conditions to measure statistical significance between the main condition of interest (CP-ISO) and the
329. other contextual conditions.

330. **3.4. Surround-Only responses:**

331. For the “cardinal” protocol, statistical significance was assessed using Z-test statistics on response
332. integrals ($p < 0.05$). For the “radial” protocol, we used a permutation test (10^4 repetitions; $p < 0.01$). Due
333. to the noisy nature and the weak amplitude of purely lateral responses, we only retained Vm
334. waveforms for which the statistical significance threshold was trespassed for at least 15 consecutive
335. milliseconds in the interval 0-120 ms.

336. **3.5. Linear predictions and Dynamic non-linearities:**

337. For the “radial” protocol, we determined in each individual case whether the actual Surround-
338. Only responses to dynamic sequences were larger than (or equal to) the sum of the temporally shifted
339. responses to each GP flashed in isolation at each location (reproducing the spatial and temporal
340. ordering of a virtual AM sequence). This linear predictor was in a first step compared to the actual AM
341. dynamic sequences before they reached the RF Center, to probe for a nonlinearity between the
342. integration of elements flashed in isolation in the surround and the actual build-up of anticipatory
343. activity during AM sequences. Because GP flashed in isolation in the close vicinity of the SDF already
344. induce significant depolarizing responses (29), we considered Surround-Only synaptic waveforms as
345. significantly larger than their “static” linear predictor, if they crossed the upper limit of the confidence
346. interval for a minimum duration of 7 consecutive ms in the interval 0-120 ms (permutation test, 10^4
347. repetitions, $p < 0.05$). A second predictor was calculated by subtracting the Center-Only response from
348. the complete AM “Surround-then-Center” response. This two-term linear predictor was compared to
349. the observed “Surround-only” AM response to test for a non-linearity between the integration of
350. contextual information in the “Near” Surround and the feedforward drive.

351. **3.6. Population analysis:**

352. In order to compare responses between cells, each individual flow pattern’s specific geometry –
 353. defined on a cell-by-cell basis according to the preferred orientation and direction of each cell – was
 354. realigned on a common “0°” reference axis (visualized by the semi-horizontal axis pointing to the right
 355. in all Figures), regardless of the absolute orientation preference of each cell. No normalization of
 356. responses was used in the “cardinal” protocol. In the “radial” protocol, the amplitude of the PSTWs
 357. and PSTHs of each cell were first normalized to the peak of the Center-Only response. Before
 358. averaging, PSTWs and PSTHs of all the cells were also realigned with respect to the onset latency of
 359. their individual Center-Only response (respectively, subthreshold and spiking), which was defined as
 360. the time of the first point (blue dot) of the average Center-Only response departing from the “blank”
 361. response mean by more than 3σ . This allowed a realignment of all normalized cell-by cell profiles and
 362. the calculus of the mean population response profile.

363.

364. **Results**

365. This intracellular study (65 cells) of Center-Surround interactions in V1 of the anesthetized cat is
 366. based on two distinct visual protocols, applied in two different sets of cells (see Methods). The first
 367. protocol, termed “**cardinal**” (Fig. 1B), recruiting both “Near” and “Far” RF surround, was applied to a
 368. first batch of 23 cells. The second series of protocols, termed “**radial**” (Fig. 1C), limiting the Surround
 369. stimulation to “Far” regions outside the SRF only, was performed on a second batch of 42 cells.
 370. Accordingly, response averages were done separately for the two visual stimulation protocols.

371. **1. Probing synaptic responses from the “silent” Surround**

372. **1.1. Spatial summation**

373. The “silent Surround” is classically defined as the region outside the minimal discharge field
 374. (MDF), where impulse stimuli do not evoke a significant spiking response. However, the intracellular
 375. mapping of synaptic responses with sparse or dense noise (SN or DN), devoid of spatial summation,
 376. shows a broader subthreshold (non-spiking) receptive field (SRF) extending beyond the border of the
 377. MDF, and often invading the opponent contrast discharge field, even in Simple cells (43, 44). This
 378. defines a Near-Surround domain, connex to the MDF, where the contribution of purely lateral synaptic
 379. input cannot be unambiguously disentangled from subthreshold feedforward activation (25).

380. The mapping of the minimal discharge field (MDF) with small light or dark squares (0.2-0.9°)
 381. showed on average a spiking core field of 1-3° of visual angle. Overall, the size of the impulse
 382. subthreshold depolarizing receptive field (SRF) of the cortical neurons recorded in this study ranged
 383. from 2.5° to 7.5° ($5.1 \pm 1.6^\circ$), for eccentricities from the area centralis between 1.1° and 8.3° ($4.0 \pm$
 384. 1.6°). This initial mapping was used to define, in a conservative way in each cell, the retinotopic
 385. imprint of the feedforward input, whether it produced a spike (MDF) or only a depolarizing
 386. subthreshold response (SRF).

387. In contrast, elongated light bars (5-12° length) flashed across the RF width axis, which increases
388. input spatial summation, elicited synaptic responses, in the same cell, originating much further away
389. from the RF center (7.1° for bars against 2.5° for SN in the example cell in Fig. 2A). Using annular
390. gratings at the optimal phase and orientation, with still larger spatial summation, our lab previously
391. demonstrated distal synaptic responses originating beyond 10° of relative eccentricity (Fig. 2B). These
392. different observations have established that the recruitment efficacy of lateral connectivity evoking
393. Surround responses strongly depends on the level of spatial summation and are selective to the
394. orientation feature of the stimulus flashed in the distal periphery (26, 27, 45).

395. -----

396. **Fig 2. A synaptic view of visual V1 receptive fields**

397. **[A] : Latency basin of synaptic responses relative to the RF Center :** Top left, spatial maps of the ON- and OFF-
398. Depolarizing Fields latencies using sparse noise (SN) mapping. Heat scale: color code for latency values (from 0
399. (black) to 200 ms (yellow)). Bottom left, 1D-mapping of ON- and OFF- PSP responses in the same cell, evoked by
400. long bars (7.1°x0.7°) flashed at the optimal orientation and positioned at different eccentricities (in ordinates,
401. ranging from -4° (bottom) to +6° (top)) across the RF width axis. Thick boxes (left ordinates) designate the
402. positions which are in overlap with the SRF mapping using SN (above, top left). Red (ON) and blue (OFF) linear
403. regressions illustrate the 1D-latency basin profiles of Surround-Only subthreshold responses. The linear fits of
404. latency versus eccentricity give apparent horizontal speeds of propagation estimates of 0.18-0.38 mm/ms for
405. ON- (red, left) and OFF- (blue, right) responses.

406. **[B] Dependency on spatial summation** (adapted from (26)) : From top to bottom, phase-reversal (2 Hz)
407. responses to disk [1] and annular gratings [2 & 3], for increasing inner border eccentricities from the
408. RF center (0° in [1], 5.6° in [2] and 10.3° in [3]). Note the strength decay and the onset latency increase in
409. Surround-Only responses [2 & 3] with eccentricity, reaching 32 ms for the “Far” Surround annulus.

410. **[C] Apparent Speed of Horizontal Propagation (ASHP) distribution :** Stacked data histograms from (26)
411. using long bars (1D-mapping, blue) or sparse noise (green). Note that most values extracted from latency
412. basin slopes range between 0.05 and 0.60 mm/ms.

413. -----

414. **1.2. Latency dependency of Surround responses with relative eccentricity**

415. In addition to the spatial extent of the RF, a pivotal observation, on which our working hypothesis
 416. is grounded, is that the further away from the MDF center, the latency of subthreshold surround
 417. responses progressively increases in a linear fashion with relative eccentricity, while the onset
 418. latency and the rising phase of those surround-responses depends on the spatial summation extent of
 419. the stimulus used to probe visual responsiveness. Fig. 2A illustrates the spatio-temporal latency
 420. maps of depolarizing and spiking responses of a V1 cell for sparse noise (top panel) and of synaptic
 421. subthreshold PSPs for optimally oriented long bars flashed at different eccentricities across the RF
 422. width axis (bottom panel). In this latter case, the 1D-plots of ON- and OFF-responses can be used to
 423. extract the slopes of the latency gradients with eccentricity relative to the RF center. These measures
 424. allow to infer estimates of the mean apparent speed of horizontal propagation (ASHP), ranging here
 425. from 0.18 and 0.38 mm/ms. When increasing spatial summation by using optimally oriented and
 426. phased annular gratings, the resulting latency shifts can increase to 20-50 ms for relative eccentricity
 427. values as large as 11°. The measured propagation speed (and conversely the onset latency of surround
 428. responses) for flashed long bars (blue histogram in Fig. 2C) appears similar with that obtained from
 429. sparse noise mapping (SN, green histogram), apart from tail values reaching larger values for long bars
 430. (ASHP mean $\pm \sigma$: (for SN, green) 0.21 ± 0.16 mm/ms; (for bars, blue) 0.27 ± 0.22 mm/ms).

431. **1.3. Apparent Motion Axial sensitivity and Orientation tuning**

432. Once the Gabor template optimizing the Center response was determined (see Methods), each RF
 433. and/or its Surround were tested with 2-stroke (Surround-Only) or 3-stroke apparent motion (AM)
 434. sequences along the cardinal RF axes (Fig. 1B). These “cardinals” axes, extending symmetrically
 435. around the RF center, correspond, one, to the “main” orientation preference axis (represented
 436. arbitrarily by the horizontal, in all the figures) and the other, to the RF width axis (vertical). For each of
 437. these axes, the orientation of the local Gabor inducer stimuli could be either similar, “ISO-RF”, or
 438. orthogonal, “CROSS-RF” to that of the RF orientation preference axis.

439. Examples of Surround-Only AM responses of the “cardinal” protocol are illustrated in Fig. 3A,
 440. whose magnitude can reach the size of the response to a low contrast input in the center (compare
 441. Surround-Only CP-ISO AM responses (red waveform) along the preferred orientation axis with the
 442. Center-Only response (black waveform)). As a reference, the center insert in Fig. 3A illustrates the
 443. mapping of the SRF border (white contour) and the ON- and OFF-discharge fields (respectively, filled in
 444. red and blue). The surround source locations of GPs used in the AM sequence partially encroach on
 445. the SRF border, but not on the MDF. The AM evoked synaptic responses are much stronger than the
 446. impulse SN response, as shown by the absence of depolarizing responses to light (lower dark red
 447. trace) and dark (blue trace) pixel stimulations, presented in the center of the lesser eccentricity
 448. peripheral Gabor location. In this example, as in most recorded RFs, the centripetal Surround-Only AM
 449. response along the preferred orientation axis (CP-ISO, left and right red waveforms) is the strongest
 450. among the responses evoked by the Surround stimulation alone : compare it with the CP-CROSS
 451. conditions along the RF width axis (top and bottom, gold waveforms), for which responses are much
 452. weaker.

453. -----

454. **Fig 3. Spatio-temporal and axial selectivity of “Surround-Only” responses to Centripetal AM flow**

455. **[A] Single Cell example** : Central inset cartoon: ON and OFF discharge fields, respectively in red and blue. White
 456. contour delineates the subthreshold receptive field (SRF). For comparison, respective positions of the Gabor
 457. inducer stimuli flashed in the surround are overlaid on the RF map. Two-stroke “Surround-Only” AM responses :
 458. Comparison of “collinear” (red) and “parallel” (gold) responses evoked respectively along the orientation
 459. preference and across the width axis of the RF, with the Center-only response (black waveform). Bottom left
 460. corner, Vm subthreshold responses for sparse noise (ON (dark red) and OFF (dark blue) waveforms).

461. **[B] Dependency of Surround-Only responses on the orientation of the inducer** : Right, top and bottom panels
 462. illustrate the Gabor inducer features and the color codes for the motion axis explored respectively in the ISO-
 463. and CROSS-configurations. The color code conventions are : ISO-RF: red for “collinear” along the orientation
 464. preference axis; gold for “parallel” across the RF width axis; CROSS-RF: cyan for “parallel” across the orientation
 465. preference axis; pink for “collinear” along the RF width axis. See [Text](#) for details.

466. -----

467. A complete study of the dependency of the Surround-Only AM responses on the GP inducer
 468. orientation relative to the RF preferred orientation was replicated in 13 cells. The average responses
 469. of this population have been computed by realigning arbitrarily the orientation and direction
 470. preference of each recorded cell respectively with the horizontal and right pole axes. The mean
 471. population tuning responses are illustrated in Fig. 3B, where the different AM flow conditions are
 472. schematized by color-coded arrows in the two right inserts. The top insert regroups the specific
 473. centripetal AM flows where the inducer is either “collinear” (red) or “parallel” (gold)) with the RF
 474. preferred orientation (ISO-RF condition). The bottom insert details the stimulation cases where the
 475. inducer is orthogonal with the RF preferred orientation (CROSS-RF: cyan along the main axis, pink
 476. along the RF width axis).

477. This study reveals two effects of the Surround contribution. The first one is a non-specific
 478. facilitation component found for all AM configurations, regardless of the orientation of the inducers
 479. relative to that of the RF. It corresponds to the fact that all centripetal Surround-Only flows, which
 480. terminate in the “Near” periphery of the RF core, recruit simultaneously synaptic input originating
 481. from the feedforward SRF as well as proximal horizontal input. The second one is orientation selective
 482. and reflects the dominance of responses evoked by centripetal flows of Gabor elements “co-aligned”
 483. with the RF preferred orientation (Fig. 3B) : the evoked depolarizing Surround-Only subthreshold
 484. response elicited by CP-ISO collinear flow along the main RF axis (red trace, horizontal axis in all
 485. figures) is, on average, 2.6 times larger than that evoked by CP-ISO- (pink) or CP-CROSS- (gold) flows
 486. along the RF width axis and by CP-CROSS- flows (cyan) across the RF main axis.

487. The classically reported “edge-detector” property of V1 neurons, as initially described by Hubel
 488. and Wiesel (46), highlights the fact that the strongest discharge is evoked by “parallel” elements swept
 489. towards the RF center orthogonally across its width axis (CROSS_width-axis configuration, gold trace,
 490. right top inset in Fig. 3B) at low speed (1-10 °/s). In contrast, the detailed comparison between the CP-
 491. ISO main-axis (red traces) and the CP-CROSS width-axis (gold traces) configurations implemented here

492. illustrates a functional switch of preferred integration axis between low-speed and high-speed
 493. recruitment of surround sources. Indeed, at high AM speed (100-500°/s), the synaptic integration of
 494. “Near” periphery was found to depend on the motion axis, revealing a spatial selectivity and
 495. anisotropy not present in the MDF mapped with light/dark impulses. Furthermore, the centripetal
 496. flow of co-aligned GPs along the RF preferred orientation axis (CP-ISO) revealed to be the most
 497. efficient in inducing a tonic subthreshold enhancement of sensory responsiveness irrespectively
 498. of the RF center stimulation (or its omission). Finally, the comparison of the CP-ISO and CP-CROSS
 499. mean subthreshold response profiles shows a clear orientation and axial bias of the “Surround-only”
 500. responses for Gabors co-aligned along the orientation preference axis (red waveforms). In contrast, an
 501. absence of local feature selectivity was found for AM along the RF width axis (pink and gold traces),
 502. with response levels similar to that evoked by CROSS-oriented elements along the RF main axis (cyan
 503. traces). In addition, the recruitment of the “Near” periphery rose significantly the level of excitability
 504. of the recorded cells (one sided Z-test above resting state, $p < 0.05$). A mean integral depolarization
 505. was apparent in 76% of cells for the CP-ISO “collinear” (red) condition, and in 55% in the “parallel”
 506. (gold) condition at high AM speed. Considering both main and width axes together, independently of
 507. the efficiency with which the “Near” surround was recruited, even spiking facilitation was observed in
 508. 59% of the cases while leaving the MDF center unstimulated.

509. Altogether, the comparative analysis between each configuration of Surround-Only stimulation
 510. validates the prediction of the "Dynamic Association Field" hypothesis, a concept defined in our
 511. previous study (29): the collinear configuration promotes input collection along the orientation
 512. preference axis, resulting in the emergence of centripetal axial direction selectivity for high-speed co-
 513. aligned stimuli.

514.

515. **2. Specificity of the interaction between “local” (inducer) and “global” (AM motion) features**

516. **2.1. Inducer co-alignment with the RF orientation promotes centripetal synaptic integration along the global motion axis**

517. The following contextual analysis focuses now on the modulatory effect that a two-stroke
518. activation of the silent Surround (along each of the cardinal axes) can produce on the response to a
519. subsequent test Gabor stimulus (the third stroke), flashed at the preferred orientation within the MDF
520. (right column in Fig. 1B). In addition to stimulations restricted to the Surround, the contextual impact
521. of the Surround was measured (in an interleaved way) by comparing the response to the full apparent
522. motion sequence terminating in, or departing from the RF (3-stroke AM, centripetal (CP) “Surround-
523. then-Center” and centrifugal (CF) “Center-Then-Surround” conditions) to the response to the test
524. stimulus in the RF (“Center-Only” condition).

525. The complete set of configurations including Centripetal (CP) and Centrifugal (CF) flows of Gabor
526. inducers either co-aligned with the motion axis along the RF preferred orientation (“collinear”), or
527. orthogonal to the RF width axis (“parallel”), was tested in 23 cells. As expected from the feature
528. characteristic of Surround-Only responses, both “collinear” and “parallel” centripetal AM flows
529. invading the RF elicited a facilitating effect on the Center test response. Considering centripetal flows,
530. a significant depolarizing facilitation by the surround stimulation could be observed respectively in
531. 95% of occurrences for “collinear” and 69% for “parallel” conditions. A similar observation was
532. observed at the spiking level, with respectively 84% of occurrences for “collinear” and 66% for
533. “parallel” conditions (one sided Z-test above resting state, $p < 0.05$).

534. Fig. 4 illustrates the case of a highly selective dependency of contextual control of the cortical
535. transfer function on the flow direction, emphasizing the functional facilitatory impact of centripetal
536. collinear (CP-ISO) flows (red profile, upper panel) proceeding from Surround to Center along the
537. orientation preference axis of the RF: in addition to the change in response integral, a significant
538. latency shortening is observed both at the subthreshold (upper waveforms) and spiking (lower filled
539. PSTHs) levels (compare with black profiles of the Center-Only response). In contrast, a late change in
540. the PSTW waveform integral, but not of its latency, is observed when the AM flow is centrifugal (CF)

541. and proceeds from Center to Surround (green and brown, bottom panel of Fig. 4). These differential
542. kinetic changes fit with those expected from a simple summation model, since CP- and CF-AM
543. sequences respectively impact the early and late phase of the response when stimulation of the
544. Surround precedes the Center or when the temporal order of stimulation is reversed.

545. -----

546. **Fig. 4 : Example of contextual modulation of the Center-response by Centripetal AM (“cardinal” protocol).**

547. Example of Center-Surround AM responses, compared to the Center-Only condition. The comparison, in the
548. same cell, between centripetal (CP: top panel) and centrifugal (CF: bottom panel) motion flows illustrates the
549. importance of the Surround-then-Center timing in the associative effect. PSTWs (top) and PSTHs (bottom) for the
550. four AM axes (red (CP) and green (CF), “collinear” along the RF orientation preference axis; gold (CP) and brown
551. (CF), “parallel” across the RF width axis. The contextual response is overlaid on the Center-Only stimulation
552. (black). Note that the contextual latency shortening and the spike discharge rate increase of the Center response
553. are observed only in the collinear Centripetal condition (top, red).

554. -----

555. Considering both centripetal and centrifugal flows, among the pool of 23 recorded cells, a strong
556. bias for “collinearity” was observed in 91 % of the cells at the subthreshold level and 95% at the
557. spiking level (the bias was averaged across the two RF sides for the same axis). In terms of magnitude,
558. the “collinear” AM flow produced the largest modulatory effects and evoked, on average, a
559. depolarizing response 2.6 times larger and a spiking response 2.0 times stronger, than the “parallel”
560. sequence condition. At the spiking level, effects varied from cells to cells, but, in most cases, they were
561. characterized by a shortening of spiking latency along the “collinear” axis for centripetal flows.
562. Changes in firing rate integral or response integral mainly affected the “collinear” axis response, but,
563. as expected from the non-specific component of Surround-only responses, facilitation was also
564. observed for the “parallel” stimulations : note the weak CROSS_width-axis “parallel” facilitation seen
565. for centripetal (top panel, gold waveforms) and centrifugal traces (bottom panel, brown waveforms of
566. Fig. 4).

567. 2.2. Differential impact of “Near” and “Far” Surround recruitment

568. In order to better delineate the contribution of the “Far” periphery, we designed a more
569. conservative stimulation protocol (the “radial” protocol, Fig. 1C) where the Surround stimulation was
570. allowed only outside the impulse SRF (and not only the MDF, as done previously in the “cardinal”
571. protocol). The spacing between GP inducers was increased from 120% of the MDF to 100% of the SRF
572. and the absence of overlap between the nearest Surround stimulus and the SRF was checked for each
573. of the recorded cells. Stimulation was no longer restricted to the main and cardinal axes but extended
574. to angular SECTORS surrounding the original cardinal axes by two neighboring ($\pm 30^\circ$) stimulation axes,
575. mimicking the spatial sensitivity of the synaptic association field (29). We also dropped, from the
576. stimulation set, the AM configurations used in the cardinal protocol for which non-specific component
577. responses were evoked (when co-varying the local inducer orientation and the motion axis). This
578. enabled us to focus on our main conditions of interest with GP elements ISO-oriented with the motion
579. axis always presented along the RF preferred orientation axis (CP-ISO and CF-ISO) while elements
580. CROSS oriented to the motion axis only referred to stimulations along the width axis of each recorded
581. cell (CP-CROSS).

582. Note here the terminology change in ISO and CROSS definitions, imposed by the radial symmetry
583. introduced in this latter protocol. When applied to the formal (cardinal) protocol, the ISO-axis
584. conditions correspond to cases where the orientation of the flashed Gabor patches is either “co-
585. aligned” with the RF preferred orientation axis (1st row in Fig. 1B; CP- and CF-ISO_main-axis, red and
586. green arrows), or cross-oriented with it, but, in that later case, co-aligned the width axis (CP-
587. ISO_width-axis, pink). Accordingly, the CROSS-axis conditions (CP-CROSS_main-axis and CP-
588. CROSS_width-axis) are respectively schematized by cyan and gold arrows for CP-AM and brown arrows
589. for CF-AM flows in Fig. 1B). In addition, in the “radial” protocol, each of the 37 cells recorded was
590. stimulated with an extended benchmark of contextual 5- to 6-stroke AM flows, richer than in the
591. cardinal protocol. The parametric systematization of the various flows of ISO-axis or CROSS-axis GP
592. sequences is detailed in each row of Fig. 1C.

Fig. 5 illustrates important spatial differences in the Surround periphery recruitment between the two protocols (“cardinal” in A; “radial” in B), by comparing the respective time-course profiles of the intracellular responses, evoked by the sole stimulation of the surround (Surround-Only, dotted traces) and by the complete AM sequence terminating in the RF center (Surround-then-Center, continuous traces). The top row in Fig. 5 illustrates the RF maps of the spiking discharge fields (ON (red) and OFF (blue)) and of the subthreshold SRF (topological union of ON and OFF depolarizing fields) delimited by a white contour. In order to focus the comparison with the stimulation axes used in the “cardinal” protocol, we illustrate, for the “radial” protocol cell (B, right panel), only the CP-ISO and CP-CROSS Sector AM configurations (first and third row, in the left column of Fig. 1C, red and gold schemes) along respectively the RF main and width axes. A straightforward observation directly emerges from the comparison of the visual field paving with Surround GPs applied in each protocol : for the same spatial viewing field size centered on each RF (20°x20°), the two Surround sources of stimulation are visible for the “cardinal” protocol, while only one - the most proximal (to the RF center) - appears for the “radial” protocol. The closest GP location in the periphery (D1 position in Fig. 1A) partially encroaches on the border of the SRF in the “cardinal” protocol, while this is not the case (by design) for any surround sources in the “radial” protocol.

This difference in the spatial overlap factor accounts for the differences in intracellular response magnitudes observed in each protocol. In the “cardinal” case (Fig. 5A), the “Near” Surround-Only stimulation evokes sizeable depolarizing responses, both for CP-ISO and CP-CROSS stimulations (dotted red and gold waveforms). Both types of CP Surround-then-Center AM flows strongly amplify the evoked PSP amplitude although the peak amplitude gain is the largest in the CP-ISO condition. In contrast, the typical behaviour observed in the “radial” protocol (Fig. 5B) shows a different profile. For a comparable magnitude of the Center-only response (8.0 mV (“radial”) vs. 7.4 mV (“cardinal”)), the purely modulatory influence of the CP-ISO AM flow restricted to the “Far” Surround was generally much weaker (2-3 times) than that seen for the “cardinal” protocol (here, 3.9 mV). In contrast to the CP-ISO condition, the CP-CROSS Surround-Only stimulation is almost inefficient in inducing a

619. contextual response (compare the dotted red and gold traces in the bottom right panel in Fig. 5B).
 620. As a consequence, in the “radial” protocol, the complete CP-ISO AM sequence (terminating in the RF
 621. center) is the only condition inducing a phase advance and a significant amplification of the early
 622. Center-only response.

623. -----

624. **Fig.5 : Differential recruitment of “Near” vs “Far” Surround between the “cardinal” vs. “radial” protocols**

625. **[A]: “cardinal” protocol, and [B]: “radial” protocol.** Top row, receptive field maps. Same convention as in Fig.
 626. 3A. Only the Surround GPs on the RF main (horizontal) and width (vertical) axis (common to both protocols) are
 627. represented within the same viewing field (20°x20°). Note the encroachment of the most proximal GPs in the
 628. “cardinal” protocol over the SRF (white contour), whereas no spatial overlap is seen in the “radial” protocol.
 629. Bottom rows, the CP-ISO (red) and CP-CROSS (gold waveforms) are overlaid for the “Surround-Only” (dotted)
 630. and the “Surround-then-Center” (continuous trace) conditions and compared to the “Center-Only” test condition
 631. (black). Insets show respectively an expanded version of the PSPs onset on a 30ms time window. Arrows indicate
 632. the change in PSP slope due to the feedforward synaptic drive triggered by the Center test stimulus. See [Text](#) for
 633. details.

634. -----

635. A mechanistic difference between the two protocols is further attested by the comparison of the
 636. rising slopes of the time-profiles of the AM responses with that of the feedforward response (Center-
 637. Only). In the “cardinal” example cell (bottom left panel in Fig. 5A), both the CP-ISO Surround-Only and
 638. the CP-ISO Surround-then-Center evoked PSPs have the same initial rising slope and latency (in
 639. absolute value terms, relative to D1 stimulation) as the Center-Only response (relative to D0
 640. stimulation), thus suggestive of a synaptic feedforward input signature. Note also that both the CP-ISO
 641. and CP-CROSS synaptic responses start to rise simultaneously in the “cardinal” case, which indicates
 642. that the “Near” stimulated periphery overlaps with the feedforward synaptic drive. In contrast, in the
 643. case of the “radial” example (bottom right inset in Fig. 5B), the CP-CROSS profile is undistinguishable
 644. from that of the Center-Only (gold and black) waveform and the initial rising slope of the CP-ISO

645. response (red) occurs much earlier and is initially weaker than that of the Center-Only response. These
646. latter features are suggestive of a slower spatio-temporal diffusion process compatible with horizontal
647. activity propagation. This qualitative comparison clearly emphasizes that preventing the closest
648. surround-location from encroaching on the SRF border leads to the disappearance of the non-specific
649. tonic component of the boosting of cortical responsiveness seen in the “cardinal” protocol.

650. Remarkably enough, on the whole population, the “radial” protocol led to a drastic decrease of i)
651. the proportion of cells showing “Surround-Only” responses (32 % (“radial”) vs. 100 % (“cardinal”), ii)
652. the magnitude of Surround responses, that never reached the peak amplitude of the Center-Only test
653. response, and iii) the evoked spiking level in response to the complete “Surround-then-Center” CP-
654. AM. Although the collinear configuration (“CP-ISO”) remained the most effective in the “radial”
655. protocol, the observation of a tonic non-specific component (seen for all conditions of the “cardinal”
656. protocol) was not reproduced for Surround-Only responses and consequently, their facilitation role
657. was weaker at both Vm and Spiking levels. A likely explanation is that, in contrast to the “cardinal”
658. protocol, the “radial” stimulation of the Surround no longer recruits as efficiently the “Near”
659. periphery, which seems to integrate both lateral and feedforward input. Importantly, the relative peak
660. amplitude and timing of those responses regarding control contextual stimulations, in sequences
661. restricted to the Surround or invading the RF Center were much more specific. Consequently, the
662. “radial” protocol appears best tailored to detect the selective contribution of purely lateral
663. recruitment of the “Far” periphery.

664. **2.3. Anticipatory “filling-in” responses (“radial” protocol)**

665. To highlight the emergence of a lateral anticipatory wave due the sole recruitment of the distal
666. periphery (Surround-Only wave) and quantify its functional role in the contextual gain control of the
667. response evoked by the feedforward drive, we determined - in the “radial” protocol - the individual
668. significance of each cell response to the Surround-only condition, using a point-by-point
669. randomization test (10^4 repetitions, $p < 0.01$). The largest proportion of cells showing significant
670. “Surround-Only” responses was found for the CP-ISO condition (12 cells (32% of the population)). A

single cell example is illustrated in the left column of Fig. 6. A complete CP-ISO sequence invading the RF Center reveals a clear boosting effect (compare continuous red (AM) and black (Center-Only) traces, top and bottom panels). In spite of the fact that the closest surround location was sparing the SN-mapped SRF, a sizeable significant change in membrane potential was still observed in the AM sequence restricted to the surround, from D5 to D1 locations, in the absence of D0 stimulation (bottom left graph in Fig. 6, dashed red trace). For this cell, the combined dynamic recruitment of the GP sources along the AM motion axis shows a progressive build-up signal which anticipates, by ten milliseconds, the onset of the feedforward signal evoked by the Center-stimulus. In contrast, the linear predictor based on individual static responses to GPs in isolation does not reach significance at the time where center-only response departs from resting activity (bottom left graph in Fig. 6; dashed green trace). Thus, in this particular single cell example, the AM sequence recruits a non-linear amplification process of subliminal sources, attesting for the role of spatio-temporal synergy in maximizing the functional impact of horizontal propagation.

Fig.6 : “Filling-in” responses evoked by “Surround-Only” AM (“radial” protocol).

The analysis here is restricted to cells where “Surround-Only” stimulation evoked a significant response (n=12, see [Text](#) for criteria). Color code: black for “Center-only”; red for “Surround-then-Center”, dashed red for “Surround-Only”. The middle horizontal insets respectively show the chronograms of the stroke-by-stroke stimulation sequences for “Center-Only” (1 stroke, filled black box, upper line), “Surround-Then-Center” (6 strokes, filled red, middle line) and “Surround-Only” (5 strokes, filled pale red, bottom line) protocols. Empty boxes indicate omitted stimuli. The time onset of each GP stroke is labeled by a thin dotted vertical line. In this figure and the following ones, the blue dot and vertical dotted blue bar on the y-axis indicate the “threshold” amplitude change of the Center-Only control curve from rest, above which statistical significance of the response is reached ($p<0.01$) for each individual cells. Their abscissa serves as a reference for the temporal realignment of the different contextual responses. **Left, top panel** : Single cell example. The complete CP-ISO AM sequence (D5 to D0) evokes a significant facilitation of the “Center-Only” Vm response (compare red and black traces). **Bottom Left** : when omitting the D0 stroke, the recruitment by the CP-ISO AM flow, although limited to the silent

698. surround (D5 to D1), still induces a depolarizing activation (“Surround-Only”: dashed red). The temporal profile
 699. of the lateral wave of activity matches the “predicted” invasion of the RF Center, had it been stimulated. This
 700. effect, in this cell, results from a synergistic interaction, since it cannot be explained by the sum of the static
 701. responses evoked by each distal GP stroke in isolation (dashed green, undistinguishable from rest activity).
 702. **Right, top panel** : Average response profiles for “Surround-then-Center”, “Center-Only” and “Surround-Only”
 703. conditions (n=12). **Right, bottom panel** : the CP-ISO Surround-Only response (mean: dotted red $\pm$ SEM: shaded
 704. area) is compared (with a different ordinate scale than in the top right panel) with the “expectation” (dashed
 705. black trace) obtained by subtracting the Center-Only (black trace, Top right) from the complete CP-ISO AM
 706. response (red trace, Top right). See [Text](#) for interpretation.

707. -----
 708. In the subpopulation of cells showing significant CP-ISO Surround-Only responses (point by point
 709. permutation test, 10^4 repetitions, $p < 0.01$), statistical analysis revealed that 6/12 cells (50% of
 710. significant cases; 16% of the entire population) showed significant anticipatory responses larger than
 711. their static linear predictor in the CP-ISO condition. For Surround-Only significant cases, the CP-ISO
 712. Surround-Only AM sequence triggered a synaptic wave riding clearly above the noise level, peaking at
 713. an average value corresponding to a third of the Center-Only test response peak amplitude for an
 714. absolute value ranging between 1 to 4 mV (average dotted red trace in top right panel of Fig. 6).
 715. Remarkably for the optimized AM speed, the Surround-Only average response profile rose peaked at
 716. the time of expectation of the Center-Only response. This strongly suggests a causal relationship
 717. between purely contextual information and its integration in the gain control of complete sequences
 718. terminating in the RF center.

719.

720. **3. Dependency of the contextual control of the cortical transfer function on the spatio-temporal coherence of the AM flow**

721. In order to systematically identify and quantify the key spatial and temporal factors of the CP-ISO
 722. AM sequence which conditions the contextual control of the cortical gain, we compared for each of
 723. the 37 cells, the CP-ISO configuration with AM sequences in which the spatio-temporal structure of the

GP presentation was altered (Fig. 1C). The statistical significance of the measures extracted from the mean Vm responses of individual cells (top panel in Fig. 7) was assessed by comparing each AM condition to the same reference (Center-Only) independently for the two criteria of onset latency and response strength changes, and in addition, in a less stringent way, for one or the other criteria (randomization test, 10^4 repetitions, $p < 0.05$). Both congruent and complementary trends were found across the three statistical criteria we used.

Fig. 7. Statistical significance of contextual response changes

Top panel, ranked distributions ($n=37$) of changes in Latency (ms, left column) and in response integral value (normalized ratio, right column) of subthreshold responses (Vm), for each SECTOR AM condition of interest (first three rows). The fourth row corresponds to the FULL-RND condition (see Text for justification). Color code, same as in Fig. 1C, schematized by appropriate icons in the right column. Abscissa, cell rank (1 to 37), done independently for each AM condition. Filled bars represent the amplitude change of “significant” individual cases (one-sided permutation test, 10^4 repetitions, $p < 0.05$). Ordinates: left column, latency change (“ Δ Latency”) measured at half-height of the Center-Only peak response; right column, change in the integral value of “significant” depolarization ($\pm 3\sigma$ from mean V_{rest}), measured from the onset of the test GP flashed in the RF Center to the point of return to baseline of the Center-Only response. The integral value change (“ Δ Response”) is expressed as a normalized ratio relative to the Center-Only reference response.

Bottom panel, each of the three histograms represents the proportions of significant cases for each AM flow condition (same color code as in Fig. 1C). Left, “ Δ latency” criteria. Right: “ Δ Response” criteria. Center inset (BOTH): all cases showing either a significant latency advance, or response integral increase, or both.

For latency changes only (ranked distributions, left column in the top panel of Fig. 7), the proportion of significant cases is three times larger for the CP-ISO condition (30%, red column in the left histogram, bottom panel) than for the other conditions. For response integral changes only (ranked distributions, right column in the top panel of Fig. 7) the effect is less selective across conditions, but remains specific of the collinear configuration, since most significant cases are found in

751. both CP-ISO and CF-ISO conditions (respectively red and green bars in the right histogram, bottom
752. panel). When pooling both criteria in a non-exclusive way (logical “OR”, bottom center inset), the
753. proportion of significant cases peaks for the CP-ISO condition (red histogram bar, 41%), while
754. remaining two times larger than for the CF-ISO condition (19%, green bar) and three times larger than
755. the other conditions (11%, gold bar for CP-CROSS; 14%, blue bar for RND-ISO). These different analyses
756. show that the CP-ISO AM flow is by far the most effective configuration to promote the visibility of
757. Surround-Center interactions.

758. For the CF-ISO condition, no latency advance effect was induced at the PSP level on the
759. population average (n=37), since the rising phase of the CF-induced Vm response, as expected, was
760. undistinguishable from the Center-Only response. Only 8% of the cells showed a significant latency
761. advance of a modest magnitude in the CF-ISO condition compared to the 30% found in the CP-ISO
762. condition (green bar vs red in the left histogram, bottom panel of Fig. 7). Conversely, contextual
763. facilitation of the Center response integral was present in a slightly larger proportion of cells (14%,
764. green bar in the bottom panel right histogram of Fig. 7). Those observations concord with those of
765. the “cardinal” protocol, since the rising phase of the CF-induced response, as expected, was
766. undistinguishable from the Center-Only response. On the other hand, the increase in response integral
767. value concords with a lasting depolarization following the center-only test peak response, as more and
768. more Gabor patches flashed at increasing eccentricity from the RF center evoke a series of lagged
769. desynchronized lateral inputs of exponentially decreasing amplitude. This first control demonstrates
770. that the spatial co-alignment of GPs is not enough in itself to induce the observed boosting effect.
771. Some form of spatio-temporal ordering is required such that an anticipatory flow from the periphery is
772. generated, which, *in fine*, will boost sensory responsiveness at the time when the test stimulus hits the
773. RF Center.

774. Since, whatever the speed, moving cross-oriented stimuli across the orientation preference axis of
775. the recorded RF were in most cases ineffective in firing the cell, we studied the impact of CP-CROSS
776. AM sequences along an angular sector restricted around the width axis (Fig. 1C: left column “SECTOR”;

777. gold condition). This however implies in the SECTOR configuration that the analysis relies on the
 778. comparison of response flows (CP-ISO vs. CP-CROSS) sweeping across different surround subregions,
 779. while maintaining the orientation of all GPs the same. Nevertheless, the absence of an orientation-
 780. selective component for centripetal flows of CROSS-oriented GPs along the main axis of the RF (CP-
 781. CROSS_main-axis, cyan traces in Fig. 3) justifies this simplification choice. In spite of these subtle
 782. protocol differences, only 11% of the cells showed a significant positive latency advance to the CP-
 783. CROSS stimulation, while none displayed any significant change in the response integral, when
 784. compared to the Center-Only test response (bottom panel, respectively left and right gold histogram
 785. bars in Fig. 7). Overall, the weak changes in latency advance or amplification of the Center-Only
 786. response found in individual cells during CP-CROSS AM flows was washed out completely when
 787. averaging across cells (RIGHT panel in Fig. 8, compare yellow and black mean waveforms). A similar
 788. conclusion is reached whether the surround was partially (SECTOR) or uniformly (FULL) recruited: in
 789. both conditions (SECTOR and FULL), the contextual mean CP-CROSS responses were almost
 790. undistinguishable from the Center-Only test response (data not shown).

791. -----

792. **Fig. 8 : Contextual Gain Control induced by centripetal-ISO AM flow (“radial” protocol)**

793. **Top** row, subthreshold response (Vm); **Bottom** row, firing rate response (spikes/s). The first three columns, from
 794. the left illustrate the boosting effect produced by a CP-ISO AM sequence (red curve, “Surround-then-Center”)
 795. when compared to the response to the test GP inducer flashed in the RF Center (black curve, “Center-Only”). The
 796. local orientation of the GP inducers in the Surround and the global AM axis are co-aligned with the RF
 797. orientation preference. The last (right) column focuses on contextual dependency of the effect.
 798. **From left to right, first column :** Single cell example, where the vertical dotted gray lines indicate the respective
 799. timing of each peripheral stroke stimulation at successive eccentricities (from D5 to D1), whereas the continuous
 800. vertical gray line indicates the onset of the “Center-Only” test stimulation (D0). The blue dot and corresponding
 801. dotted line give the latency of the first point in time where the “Center-Only” response departs significantly from
 802. the resting state ($p < 0.01$). **Second column** from the left, population averages for the CP-ISO (red) and
 803. the Center-Only (black) conditions. Averaging is done in two steps, first across trials for each cell for the same

804. context condition, then across cells after realigning individual mean waveforms around a common onset latency
 805. of their “Centre-Only” response (“0” mark of the “Relative Time” abscissa, blue points in left panels). Response
 806. amplitudes are normalized relatively to the peak of the “Center-Only” response. The **third column** illustrates,
 807. for “significant cells” only (see Fig. 7), the difference in rising phases and onset latencies between the CP-ISO
 808. (red) and Center-Only responses on an expanded time basis. The mean $\pm$ SEM value envelopes are respectively
 809. indicated by a continuous curve and a shaded area. The third column shows the same trend for the whole
 810. population, all cells included, irrespectively of the significance criteria. **Right column**, the significance analysis is
 811. extended to cells which showed significant Surround-only responses (see [Text](#) for criteria: subthreshold: n=20;
 812. spiking: n=10). The contextual averages (color code same as in Fig. 1C) show that CP-ISO (red) is the only
 813. condition where a change in onset latency is observed, both at the Vm (top) and spiking levels.

814. -----

815. In a third control condition, the same retinal SECTOR space as in our CP-ISO condition of interest
 816. was stimulated with the same GPs (i.e., with the same number, features, and stimulus energy
 817. distribution) but the coherence of the flows was pseudo-randomized both in space and time. Such
 818. RND-ISO condition induced a slight facilitation effect on average, although significantly smaller than
 819. the one seen in the CP-ISO condition. We explored the possibility that this partial effect could be of
 820. residual nature and come from an insufficient level of randomization achievable in the SECTOR
 821. stimulation. Indeed, the number of visited nodes (i.e. GPs) is rather low (n=26), with the additional
 822. constraint that the last Gabor patch in the sequence had to be the one flashed in the Center. Note
 823. that, in contrast to coherent-AM sequences, GPs flashed during each step of the RND-ISO AM
 824. sequence could belong to any ring of eccentricity, thereby increasing at each step of the AM sequence
 825. the probability to find D1- (or D2-) to center stimulations (see [Methods](#)). Close examination of
 826. individual cell recordings showed that the slight facilitation most likely reflected the fact that in some
 827. RND-ISO trials, the penultimate GPs were presented occasionally by chance at the D1, or even D2
 828. eccentricity (Fig. 1A), just one stroke ahead of the RF center stimulation. We concluded that the Sector
 829. RND-ISO sequence often recruited facilitating two-stroke AM Surround-Center pairs whose effect has
 830. already been reported (see fig. 7 in (29)). To dilute the remnant impact of proximal-to-center

831. interactions seen in the RND SECTOR condition, we used, as a more randomized control, the FULL
832. stimulation configuration in which the probability to find such co-aligned D1 (or D2) GP followed by
833. the RF center stimulation during the entire stimulation protocol was lowered by increasing the
834. number of possible peripheral node locations (from $n=26$ to $n=52$), thereby increasing the level of
835. randomization of the AM sequence. In the RND FULL mode, the stimulation was not restricted to
836. retinal sectors on both sides of the RF but was extended isotropically to its entire Surround (bottom
837. right blue icon in Fig. 1C). In a limited fraction of the cells, response to the FULL RND stimulation still
838. displayed a slight facilitatory effect (11% for latency change and 3% for response gain) compared to
839. the Center-Only test response (blue columns, in respectively the left and right histogram bars in the
840. bottom panel of Fig. 7), and this effect disappears when averaging across cells (compare average blue
841. and black waveforms in the right panel in Fig. 8). We conclude that the contextual boosting of the
842. cortical transfer function was largely washed out by the reduced probability of observing collinear
843. proximal activation in the FULL RND sequences, resulting from the more extensive randomization of
844. the flow’s spatio-temporal coherence than in the SECTOR RND condition.

845. Let us focus more in depth on the CP-ISO condition. The left column in Fig. 8 illustrates the typical
846. contextual behaviour observed for Vm and spiking responses at the single cell level for the CP-ISO
847. configuration in the “radial” protocol, when compared to the Center-Only condition: the AM CP-ISO
848. sequence produces an anticipatory depolarizing wave that shortens the onset latencies of both the
849. rising phases of the PSP (upper row) and the spiking response (bottom row), by respectively 14.7 and
850. 16.3 ms. For that particular example, both a progressive build-up of a subthreshold depolarization and
851. an anticipatory firing response are observed at early latencies, but this ramp-up feature was not
852. systematically observed in all cells. At the population level, we found that centripetal flows composed
853. of Gabor elements co-aligned with the global motion path along the RF main axis (CP-ISO) resulted in
854. an overall boosting of the neural response compared to that evoked by the test Center stimulus alone.
855. This finding is illustrated in the second column (from the left) of Fig. 8. Note here that the PSTW and
856. PSTHs realignments (see Fig. 6 legend) are done separately for the averaging since a few millisecond

857. integration lag is found between the absolute measurements of significant onset times for Vm and
858. spikes for the Center-Only responses (see the causal shift in the vertical dotted blue lines in the single
859. cell example). On average ($n=37$), the CP-ISO stimulation, in the SECTOR condition, resulted in an
860. overall latency shortening and a slight amplification of the depolarizing subthreshold response
861. envelope (Vm, upper row). It also led to a reduction in latency of the spiking discharge (third column,
862. bottom panel) in cells where spiking activity evoked in the Center-Only condition was significant
863. (permutation test, 10^4 repetitions, $p<0.05$; $n=22$).

864. In order to better quantify the effect, we restricted, in a second step, the averages to the group of
865. “significant” cells for which significant changes in latency (Δ latency) and/or strength (Δ response
866. integral) of the subthreshold component of the Vm response were induced by the CP-ISO AM flow (see
867. Methods and Fig.7). Results show that latency change and response integral modulation by the
868. centripetal AM flow significantly facilitated responses of 41 % of the cells (15/37) of the CP-ISO
869. condition. The third column in Fig. 8 focuses on the rising phases of the CP-ISO and Control
870. waveforms, and illustrates, with an expanded time basis, the significant changes in Vm and spiking
871. latencies. Note that the quenching around the “0” time abscissa, seen for the Center-Only responses,
872. results from the realignment process applied before averaging (see Methods).

873. To further demonstrate the contextual boosting specificity concomitantly at the synaptic and the
874. firing levels, we tried to maximize the population size. For this last analysis, we added - to the pool of
875. CP-ISO “significant” cells (based on Fig. 7 criteria) – the contingent of cells for which significant
876. responses could be elicited by an AM flow stimulation limited to the Surround (permutation test, 10^4
877. repetitions, $p < 0.01$; see Methods). This pooling increased the number of significant cases from 15 to
878. 20 cells for subthreshold analysis, and 6 to 10 for spiking analysis (one of the additional cells was not
879. spiking). Once again, in congruence with the statistical analysis of Fig. 7, the largest proportion of
880. significant Surround-Only responses was found for the CP-ISO condition (CP-ISO: 12/37 cells, 32%; CF-
881. ISO: 22%; CP-CROSS; 8%; RND-FULL: 11%). The right column in Fig. 8 shows that the phase advance
882. effect is selective of the CP-ISO condition, where the mean Vm (top) responses, averaged across all

883. “significant” cells (n=20 for Vm) indicate an average phase advance of 8 ms and a mean Vm response
 884. integral increase of 31%. A similar contextual phase shift is observed at the spiking level (bottom).
 885. Altogether, our intracellular results demonstrate that a build-up of anticipatory synaptic activity is
 886. observed by sequentially recruiting local inducers co-aligned with the RF orientation axis in a
 887. centripetal way. The efficiency with which the closest surround location is recruited impacts the
 888. strength of the contextual modulation. In particular, the “Near” periphery recruitment of the
 889. “cardinal” protocol points to a bias for CP-ISO AM flows along the RF preferred orientation axis,
 890. superimposed over a non-specific facilitation component observed, at both Vm and Spiking levels for
 891. all contextual stimulation conditions. Conversely, the more precise recruitment of the “Far” Surround,
 892. achieved in the “radial” protocol, points to the selective control of the cortical gain by the CP-ISO
 893. context. This specificity truly highlights a spatio-temporal requirement in Surround recruitment in
 894. order to boost sensory responsiveness. This further emphasizes the critical need of spatial and
 895. temporal synergy between each distal surround source synaptic impact with the synaptic feedforward
 896. volley corresponding to the Center-Only drive (Fig. 1A).

897.

898. **4. Timing specificity in Predictive “filling-in” responses and Surround-then-Center interactions**

899. **4.1. Synaptic mechanisms involved in predictive filling-in responses (“radial” protocol)**

900. The time-course of the average contextual responses for cells that displayed significant responses
 901. to the sole stimulation of the Surround, is compared in Fig. 9 between the CP-ISO AM SECTOR
 902. configuration (red trace) and the three other flow configurations (light green for CF-ISO, gold for CP-
 903. CROSS and blue for FULL RND-ISO). At the subthreshold level, the CP-ISO Vm response amplitude is
 904. slightly amplified and its rising phase (measured at half height of the control peak response)
 905. consistently leads by a 7 ms advance from the other conditions (top left panel, Fig. 9). At the spiking
 906. level, peak values are undistinguishable, but a clear 15 ms advance only appears in spike initiation of

907. the CP-ISO condition. Additionally, the sustained depolarization observed for the CF-ISO condition
 908. departing from the RF center is not translated at the spiking level, in contrast with the typical profile
 909. observed for the same condition in the “cardinal” protocol (compare green and black waveforms in
 910. the bottom left panel of Fig. 9, and filled histogram in the bottom panel and left part of Fig. 4).
 911. Therefore, it appears that the “radial” protocol choice to avoid the “Near” periphery and restrain the
 912. closest surround stimulation to the “Far” Surround enhances the specificity of the CP-ISO induced
 913. facilitation, since phase advance and amplification of the Center-Only test response (black traces) are
 914. only found for that specific condition. The averaging almost completely washed-out the non-specific
 915. components found in the other AM conditions when using the “cardinal” protocol. Accordingly, in the
 916. “radial” protocol, all other contextual response profiles (CF-ISO (green), CP-CROSS (gold) and RND-ISO
 917. (blue)) are undistinguishable from Center-Only responses.

918. -----

919. **Fig. 9 : Mechanistic analysis of the “Filling-in” contribution to contextual gain control.**

920. **Left**, contextual gain control analysis, restricted to the population of cells (n=12) showing significant “filling-in”
 921. responses. Mean responses, averaged for each AM flow pattern (CP-ISO (red), CF-ISO (light green), CP-CROSS
 922. (gold) and RND-ISO (blue)) are represented at the Vm (top panel) and spiking levels (bottom). Same color code as
 923. in Fig. 1C. The selective latency advance and amplification of the subthreshold response induced specifically by
 924. the CP-ISO condition (top, n=12) translate at the spiking level in cells displaying spiking activity (bottom, n=7).
 925. **Right**, comparison of the contextual time course of Surround-Only responses with the predicted contribution of
 926. the Surround according to an additive model. Top, observed traces (n=12); Bottom, linear predictors of the
 927. Surround-Only responses obtained by subtracting the “Center-Only” trace from the “Surround-Then-Center”
 928. response. The predicted profiles were calculated independently for each contextual condition (same color code).
 929. The averaging process was extended to all cells showing a significant contextual change in latency and/or
 930. response integral (n=15, see criteria in Fig. 9). The expected occurrence of the response evoked by the
 931. omitted Center stimulus is indicated by a grey shaded temporal window. The time abscissa of the peak of the
 932. “Center-Only” stimulus response is indicated by a thin vertical bar.

933. -----

934. The detailed comparison of the relative time-course of “filling-in” subthreshold response
 935. contributions between the different AM flow conditions (Fig. 9, top right panel) shows that the
 936. synaptic (Vm) contribution of the “silent” periphery is the largest for the CP-ISO condition (red). Most
 937. remarkably, it is temporally highly selective and peaks precisely at the expected time of occurrence of
 938. the Center-Only response onset (“zero” relative time; see the dotted red trace in top right panel of Fig.
 939. 6). The central issue addressed here is the temporal specificity of each purely contextual response and
 940. their respective impact on the contextual gain control.

941. Indeed, this does not mean that other contextual flows are ineffective in modifying the
 942. subthreshold baseline, such as the random (RND-FULL) configuration, which shows a depolarizing
 943. plateau (blue trace) preceding the onset of the expected Center-Only response. This initial bump is
 944. compatible with the cumulative invasion (across randomized strokes) of lateral activity and
 945. corresponds to a non-null probability of stimulation by chance of the proximal periphery of the
 946. subthreshold SRF. However, in contrast to the CP-ISO AM sequence, it collapses towards the baseline
 947. before the expected onset of the Center-Only response. For the CF-ISO condition (green trace, top
 948. right panel in Fig. 9), a mirror activation pattern regarding the Center-Only onset response is observed:
 949. starting from rest, the transient CF-ISO Surround-Only contribution growth appears only after a delay
 950. (30-35 ms), slightly after the peak of the Center-Only response had the test stimulus been presented,
 951. before displaying a progressive depolarization decay lasting up to 250 ms. This decay phase is
 952. interpreted as indicative of distal input weakening and desynchronization, the further away from the
 953. RF center (as expected from the stimulus design). In contrast, the CP-CROSS AM sequence synaptic
 954. integration is almost ineffective (gold traces). The magnitude of its peak amplitude is several folds
 955. lower than that observed in the “cardinal” protocol, reaching a peak value of only 8% of the Center-
 956. Only peak response (compare gold traces in Fig. 3, 5A vs. Fig.s 5B and the top right panel in Fig. 9). This
 957. argues once again for a “non-specific” component of the response, best seen in the “cardinal”
 958. protocol, that crucially depends on whether the most proximal peripheral Gabor patch encroaches on
 959. the SRF border or not. Note that, in spite of the fact that predictors of the Surround modulatory effect,

960. obtained by subtracting the feedforward response to the contextual response (“Surround-then-
961. Center” *minus* “Center-Only”, shown in the bottom right panel of Figs. 6 and 9), could be computed
962. even in cells whose recordings did not show significant “Surround-Only” responses, a striking similarity
963. is apparent in the overall temporal profiles of top and bottom panels of Fig. 9. This isomorphism
964. globally supports on average a linear additive model of Surround and Center influences integration
965. (although some cells behave non-linearly, as shown in Fig. 6).

966. In summary, the CP-ISO condition is the only stimulation context where the time-course of the
967. Surround-Only contribution matches precisely the time-course required to interact with the feed-
968. forward activation window (shaded area, bottom right panel in Fig. 9) and define an effective “spiking
969. opportunity window”. In contrast, in all other flow conditions, Surround-Only contribution is out of
970. sync with the feedforward drive and cannot exert mechanistically some form of additive gain control
971. of the test feedforward response. Crucially, the CP-ISO exclusivity of this precise time-localized
972. concentration in depolarizing activity power of purely contextual information actually explains the
973. selectivity of the contextual gain during complete sequences terminating in the RF center. This
974. extension in the temporal domain explains that those subthreshold synaptic responses “at the right
975. place, at the right time” can be viewed as a dynamic form of a neural correlate of “filling-in”, intrinsic
976. to V1, propagating some kind of prediction of the spatio temporal profile of the next stimulus to come.
977. We therefore interpret those waves as indicative of a neural process of “anticipation” in the cortical
978. retinotopic region for which the “expected” visual feedforward synaptic volley is missing, indicative of
979. a running Bayesian estimate based on the recent stimuli statistics already presented in the Surround.

980. **4.2. Dependency of the spiking latency advance on the temporal phase between the Feedforward and Horizontal input waves (“cardinal” protocol)**

981. The timing constraints of our protocols have a dual source: i) the synaptic activation from the
982. surround displays a temporally constrained profile in latency basin (Fig. 2), and ii) the order of the
983. sequential stimulation (centripetal & centrifugal) in the Surround (Fig. 4). In order to better quantify
984. these issues, the onset latencies of the postsynaptic potentials evoked independently in the Center-

985. Only and Surround-Only conditions were measured in the “cardinal” protocol and temporally
 986. realigned on a common reference, defined as the time at which the Center-stimulus should have been
 987. shown in the considered Surround-only 2-stroke AM sequence. The subtraction between the two input
 988. onset latencies will be referred in the rest of the text as the phase between feedforward and
 989. horizontal inputs. In spite of its weaker specificity, since the “cardinal” protocol almost systematically
 990. induced significant responses for sequences limited to the surround and strong tonic responses at
 991. both sub- and suprathreshold levels during complete sequences stimulating the center, we used the
 992. measured onset latencies of this protocol to maximize the number of cells for this analysis. This latter
 993. was however restricted to instances where both “Surround-Only” and “Surround-Then-Center”
 994. responses were tested for each condition, in the same cells. The interest of such quantification is to
 995. give an objective measure which allows the direct comparison of the effects of different associative
 996. sequences realized for a given cell as well as across various cells (Fig. 10).

997. -----

998. **Fig. 10 : Causal impact of the temporal phase between feedforward and horizontal input on the spiking latency change (“cardinal” protocol)**

999. **Left panel :** Pooled data from the “radial” (brown), and “cardinal” (orange) protocols (this study) and from the
 1000. “2-stroke” study by (29) (beige). Note that most apparent speed of horizontal propagation (ASHP) values,
 1001. extracted from intracellular latency basin slopes with relative eccentricity, range between 0.05 and 0.60 mm/ms
 1002. (with a peak between 0.10 and 0.30 mm/ms). Mirror histogram (pointing downwards) : pooled data from (26)
 1003. using long bars (1D-mapping, blue) or sparse noise mapping (green). **Right panel:** For each individual cell
 1004. recorded in the “cardinal” protocol, the latencies of Center-Only and Surround-Only Vm responses are measured
 1005. and subtracted, defining the temporal phase between the “horizontal” and “feedforward (FF)” inputs. The
 1006. scatter plot shows the relationship between the input phase and the resulting change in spiking latency of the
 1007. recorded cell produced by the AM modulation (ordinate axis). Symbols for the centripetal conditions : “x” in gold
 1008. color (CP-CROSS-parallel) and “+” symbol in red color (CP-ISO-coaligned). Symbols for the centrifugal condition :
 1009. “*” brown star (CF-CROSS-parallel) and green diamond (CF-CROSS-coaligned). In grey, bilinear fits. See [Text](#) for
 1010. details. Note a significant reduction in spiking latency when the horizontal input is integrated post-synaptically
 1011. ahead of the feedforward drive by 5-25 ms (phase advance, leftwards). The scatter plot data are projected on

1012. the x-axis (top row) or on the y-axis (right column) as Gaussian KDE fits. The color of the KDE distributions follow
1013. the convention of the “cardinal” visual stimulation protocol (Fig. 1B).

1014. -----

1015. When pooling all cells (n=23 cells, 67 measures), the distribution of input phase relationships
1016. ranged from +25 ms of phase advance to -50 ms of phase lag between horizontal and feedforward
1017. input waves at the subthreshold level (abscissa in the bottom-right scatter plot of Fig. 10). As
1018. expected, a strong bias in the distribution was observed in favor of phase advance of the Surround
1019. input for the centripetal sequences (gold “x” (CP-CROSS) and red “+” (CP-ISO) symbols) and delayed
1020. activation for the centrifugal sequences (brown “*” (CF-CROSS-parallel) and green diamond (CF-ISO-
1021. coaligned) symbols). At the spiking level, the latency shortening of the contextual (Surround + Center)
1022. output, compared to the Center-Only condition, appears crucially dependent on this input phase
1023. relationship: it was only observed for centripetal condition, i.e. when the Surround response onset
1024. (the horizontal input), preceded in time the Center-only response onset (the feedforward (FF) input).
1025. The intercept of the grey bi-linear fit, shown in the scatter plot of Fig. 10, has been optimized by two
1026. half-regression lines independently of the stimulus conditions (taking all the data points together). The
1027. correlation optimization results in a partition of the data cloud in two regions: one (on the left side)
1028. where the horizontal input lags in phase the feedforward drive, and for which no significant trend is
1029. observed; the other (on the right side), where the horizontal input is integrated postsynaptically ahead
1030. of the feedforward drive by 5-25 ms. In the ordinate domain, a significant reduction in spiking latency
1031. is observed (latency advance pointing upwards on the y-axis), reflecting in an almost linear way the
1032. phase advance of the synaptic echo of the horizontal input relative to that of the feedforward drive
1033. (“0” abscissa).

1034. The Gaussian kernel density estimator (KDE) of the input phase distribution (along the x-axis,
1035. above the scatter plot) clearly shows that the depolarizing input wave evoked by a collinear pair of
1036. stimuli flashed in a centripetal sequence in the “Near” periphery (CP-ISO, in red) was arriving on
1037. average earlier (17 ms from the scatter plot projections; 9 ms for paired data) than when the stimuli

were oriented orthogonally to the width axis path (CP-CROSS, in gold). This phase difference at the subthreshold level was significant in 65% of the cells where both Surround-Only and Surround-then-center conditions were tested for CP-CROSS and CP-ISO conditions (Z-test from resting state, $p < 0.05$). Note that, in some cells, the latency advance at both Vm and Spiking levels of the CP-CROSS stimulation (gold symbols) is non-null. However, the average 9 ms difference in subthreshold responses of CP-ISO and CP-CROSS conditions of the “cardinal” protocol corresponds to the 8 ms latency advance (between CP-ISO and Center-Only response), found for the CP-ISO significant subpopulation of “significant” cells in the “radial” protocol. Note that, for this precise contingent, the latency advance component of the CP-CROSS response was undistinguishable from the reference (Figs 7, 8 and 9).

Only centripetal collinear CP-ISO sequences could induce significant shortening in output spiking latency, by an advance as large as 30 ms. As shown by the KDE distribution on the y-axis (right of the scatter plot), the median latency reduction observed for the collinear axis during a centripetal stimulation (red line on the shaded red envelope) was 11 ms. In the other conditions, either centrifugal or centripetal “parallel” along the RF width axis, no significant latency advance could be seen: the three other distribution fits are all centered on a null latency change. At the spiking level, the median difference between the onset latency of CP- and CF-conditions is of 13 ms (respectively, red and green lines).

Although a significant difference in the distribution of surround modulation of the depolarizing and spiking responses is found between “parallel” and “collinear” conditions, no significant difference other than latency change could be revealed when comparing the centripetal vs. centrifugal conditions of the “cardinal” protocol. On average, the integral values of centripetal depolarizing and spiking responses (measured over a 100 ms window) were respectively 1.1 and 1.2 times larger than that of centrifugal responses. At the Vm level, this modest change is likely to be due to the broad duration of surround responses (130 ms) because of the strong response evoked by the closest GP in the “Near” periphery and to the existence of multiple phase relations between lateral and feedforward input

1064. during the time course of the associative process. This finding is indeed replicated in the “radial”
 1065. protocol, with an average facilitation of the center-only response integral difference of only 10%
 1066. between CP- and CF-ISO responses (Fig. 8 and Fig. 9, top right panel). At the spiking level, this modest
 1067. difference is likely linked to the shorter duration of stimulation (16 ms) used in the “cardinal” protocol,
 1068. opposed to the average 30 ± 9 ms stroke duration of each GP used in the “radial” one, for which
 1069. facilitation of the center-only integral response was not observed, probably because of the refractory
 1070. period of cells that were already stimulated in the center of their receptive field.

1071. **4.3. Synergy depends on the relative match between apparent motion and intracortical horizontal propagation speed**

1072. A subtle difference between the two types of protocols is that the AM speeds used in the “radial”
 1073. protocol depended on the GP duration and on the size of the SRF and not only on the size of the MDF
 1074. (as this was the case for the “cardinal” case). This finer speed tuning was adjusted to the
 1075. characteristics of each individual cell since the response latency and strength of evoked responses
 1076. both depend on the stroke duration and the distance between strokes. For the 37 cells of the “radial”
 1077. protocol, the average visual stimulation speed was of 189 ± 47 °/sec, (ranging from 72 to 312 °/s),
 1078. hence below the average speed of 329 ± 101 °/s (range 175-500 °/s) used in the “cardinal” protocol.
 1079. Note that despite this difference, the global ASHP distributions reported in the “radial” and “cardinal”
 1080. protocols overlap closely with the overall range of distributions reported in (26) and (29) (mirror
 1081. histograms in left panel of Fig. 10). A detailed comparison shows that the inferred speed of laterally
 1082. conveyed activity is slightly accelerated for “dynamic” sequences of AM flows recruiting the periphery
 1083. (top of the histogram) than for “static” flashed stimuli measures (bottom), peaking respectively at
 1084. 0.175 and 0.125 mm/ms. Those results point to the notion that the speed of laterally conveyed activity
 1085. is not completely hard-wired but depends partly on the type of visual stimulus used. Therefore, higher
 1086. levels of spatio-temporal coherence along the motion path slightly increases the speed of laterally
 1087. mediated activity, leading most likely to a cumulative shortening of the response onset latency at each
 1088. updated locus of stimulation of the AM path in the cortex, a phenomenology already reproduced in

1089. simulations of nested horizontal propagation (47).

1090. Functionally, a critical prediction of our “working hypothesis” is that the visibility of the lateral
1091. contextual modulation of the feedforward input should therefore increase when the speed of the AM-
1092. evoked wave in cortex grows closer to horizontal propagation speed. Focusing on the SECTOR
1093. configuration of the “radial” protocol, we studied more in depth the impact of the CP-ISO AM kinetic
1094. effects on synaptic integration in V1 in a subset of twelve cells, by comparing, in each of these cells,
1095. the impact of AM sequences of various speeds. The speed of lateral connectivity recruitment was
1096. controlled in a graded way by introducing temporal delays between GPs strokes (detailed in the
1097. chronograms in the bottom panel of Fig. 11). Each cell “optimal” speed of periphery recruitment was
1098. taken as the 100% reference speed, and was lowered to 70%, 50% and 30% in a pseudo random
1099. fashion in the same cell.

1100. -----

1101. **Fig.11 : Dependency of the Contextual effect on the speed of the AM flow :**

1102. **Bottom**, the chronograms depict the 4 inter-stroke interval conditions used in each cell to probe the temporal
1103. dependency of the interaction between the horizontal and the feedforward synaptic waves (color code reddens
1104. with speed value). The exact value of the “optimal” reference speed (100%) is defined on a cell-by-cell basis.
1105. Mean speed values, averaged across cells (n=12), are given left of each chronogram. **Top**, population averages
1106. for the CP-ISO SECTOR condition. All individual responses are realigned with the Center-Only response onset. The
1107. overlaid waveforms, averaged across cells, allow the comparison of the time-course of the response for the
1108. optimal speed value (red) with that observed for various proportional reductions of the AM flow speed (from top
1109. to bottom: 30% (dark orange), 50% (orange) and 70% (light orange)). The contextual response modulation
1110. amplitude decreases proportionally to the AM speed reduction from its optimal value.

1111. -----

1112. The comparison of the average contextual PSP response profiles of this subpopulation for
1113. incremental AM speeds (30%, 50%, 70% and 100% of the “optimal” value) highlights a cumulative
1114. speed-dependent anticipatory recruitment of the periphery, with a bumpy stairway-like profile
1115. preceding the main response peak (top panel in Fig. 11). Crucially, the overlay of response profiles for

different speeds suggests a progressive merging of lateral inputs impinging on the central target RF, from weaker amplitude and asynchronous early responses at lower speed to larger amplitude and synchronous “in-phase”-summation with the feedforward drive (Center-Only, black curve in Fig. 11) when approaching the “optimal” AM speed. As speed value grows (from 30% (light orange) to 100% (red) of the optimal speed), lateral influence gets progressively synchronized when it reaches the RF center. This is attested by the presence of dissociated bumps (preceding the Center response) at slower speed, which likely reflects sequences of asynchronous activation by the distal surround sources. In contrast, at the “optimal” speed, the precise time-concentration increase in depolarizing activity power enables a more efficient interaction with the center-only response, thereby boosting in a causal way the feedforward PSP. This result clearly emphasizes the crucial timing of synaptic recruitment in the Surround, which controls the emergence of synergy between long-distance (orange arrows in Fig. 1A) and cascades of shorter neighbor-to-neighbor links (grey arrows in Fig. 1A) along the AM path. We conclude that “in-phase” summation of lateral inputs with the predicted time of the feedforward drive produces the shortening of latency and amplitude amplification reported during CP-ISO flow at high AM speed.

Altogether, our results show that facilitatory contextual control of V1 responses is optimized along the orientation preference axis when the global motion speed lies within the range of visual flow speed predicted from the apparent conduction velocity of horizontal connectivity. For slower motion, the horizontally-driven facilitation effect disappears and stimuli cross-oriented to the motion path, presented across the width axis, remain the best drivers of cortical cells. We conclude that the axial preference of V1 cells shifts abruptly by an angle of 90 ° when the motion speed switches from 2-20 °/s to 100-250 °/s.

In summary, the spatial congruence of the elements regarding the preferred orientation axis, the spatio-temporal coherence of the flows regarding the RF center (centripetal), the speed of recruitment of the periphery and the precise timing selectivity of Surround-only responses, all suggest that some form of peripheral subthreshold “prediction” is generated internally in V1, to interact, within the

1142. proper spatio-temporal window, with the feedforward Center-Only synaptic volley. These highly
1143. selective features justify, to our view, the qualification for the existence of neural correlate of
1144. “predictive filling-in” in V1, to be distinguished from a non-specific anticipatory depolarizing spread.
- 1145.

1146. Discussion

1147. Most studies of contextual modulation in the early visual system are based on synchronous
 1148. Surround and Center stimulation, pointing to mixed suppressive and facilitatory effects (13, 14, 48-53).
 1149. We document here a dynamic regime of asynchronous Surround-Center activations, of specific speed
 1150. and spatial anisotropy, which, under precise timing and co-alignment conditions, reveals a facilitatory
 1151. form of contextual cortical transfer function control. This effect, which links global motion direction
 1152. and local orientation, is strong enough in the anesthetized brain to shorten spiking response latency
 1153. by a few tens of milliseconds and shift the axial preference of V1 cells for saccadic-like speed, favoring
 1154. contour integration along the orientation preference axis.

1155. 1. Orientation anisotropy, Motion streaks and Speed sensitivity

1156. The dependency on co-alignment and motion along the RF preferred orientation axis reported
 1157. here correlates with the anatomical bias for iso-oriented long range connections described in higher
 1158. mammalian visual cortex (*cat*: (54-56); *tree shrew*: (57-59); *macaque* : (60, 61); *squirrel monkey* : (62)).
 1159. At the functional level, it fits with the concepts of the perceptual “Association Field” in humans (4),
 1160. the neural “facilitation field” in the behaving NHP (11, 63) and the synaptic “Dynamic Association
 1161. Field” in cat V1 (29). In terms of efficiency, the requirement of maximizing the spatio-temporal synergy
 1162. from the Surround corroborates with the recruitment impact of long-distance iso-tuned interactions
 1163. visualized with imaging techniques at the mesoscopic level (40).

1164. Importantly in V1 neurons, the integration axis (the RF preferred orientation) for which the
 1165. strongest responsiveness modulation by fast (150-250°/s) apparent motion is observed, is “orthogonal”
 1166. to the preferred directional axis of V1 neurons (the RF width axis) when probed with slowly moving
 1167. bars and full field gratings. Classically, area 17 (V1) receptive fields are best activated by slow motion
 1168. across the RF width axis (1-2 °/s in (46); 3-10 °/s in (64), but quantitative studies however reveal a zoo
 1169. of speed tuning selectivities in V1 ((65-67); review in (68)). Among these, “parallel motion direction
 1170. selective” neurons could provide a potential substrate of the effects reported here. However such

1171. trigger features are classically found in higher visual cortical areas dedicated to global motion (type II
1172. MT cells (69)), but not in V1. In contrast, Geisler and colleagues hypothesized, then described, a
1173. specific class of cells in V1 responding to Gaussian blobs, named “streak” detectors, oriented in the
1174. direction of motion (70, 71). To account for disambiguation of motion direction, Geisler introduced an
1175. hypothetical multiplier circuit between direction selective and parallel detectors, whose existence is
1176. still to be demonstrated (70). Realistic estimates for the speed threshold above which “motion streak”
1177. operates point to medium range values, around 20-60°/s for cat and 10-20°/s for monkey (inferred
1178. from (72)). This “streak” effect, however, depends on the test stimulus, i.e. small isotropic Gaussian
1179. blobs, critical to avoid recruiting side-inhibition, and is absent for oriented plaid patterns (71). Other
1180. studies reported related findings: Orban and colleagues showed that spot directional tuning shift by
1181. 60-90° above a speed threshold, whereas bar tuning remained invariant (68, 73). Intrinsic optical
1182. imaging experiments - combining textures tiled with small bars and independent motion components
1183. conclude to a complex dependency of orientation domains recruitment on local motif length and
1184. motion speed (74). Similarly, 90° shifts in orientation domains were described for moving dot noise
1185. above 14.5°/s in cat area 17 (75).

1186. In contrast, the 90° shift in axial motion sensitivity reported here is found at much faster
1187. (saccadic-like) AM speeds (>50°/s), and rely on the same local inducer (oriented Gabor) shifted in
1188. space and time. It is the precise time-lagged recruitment of Surround-then-Center synaptic inputs, that
1189. conditions the contextual amplification and the phase advance of the Center response. Both the
1190. binding specificity of the local (orientation) and global (motion axis) features of the AM flow, on the
1191. one hand, and the match between the optimal AM speed and ASHP values, on the other hand, support
1192. the view that the main player is long-range horizontal connectivity intrinsic to V1.

1193. **2. Novelty of the study**

1194. The novelty of our findings is several fold : 1) these lateral diffusion effects recorded in the
1195. anesthetized, hence non-attentive, animal are likely to be intrinsic to V1 and do not require behavioral

1196. attention and top-down control from higher cortical areas (weakened by anesthesia) ; 2) they depend
 1197. on the spatiotemporal coherence of the AM sequence and grow with flow speed until matching the
 1198. apparent speed of horizontal propagation (ASHP) in V1; 3) in that range of speed, they produce a shift
 1199. by 90° of axial motion sensitivity, which becomes co-aligned the preferred orientation RF axis; 4) they
 1200. provide evidence for an internally-generated propagation process, binding local (orientation and
 1201. position) and global (motion and direction) features; 5) they constitute a plausible neural substrate of
 1202. psychophysical effects in humans reporting a perceptual bias in speed estimate for collinear motion
 1203. (76).

1204. **2.1. Intra-V1 horizontal diffusion vs. cortico-cortical feedback**

1205. Conventional models of visual cortical processing assume that complex computations, such as
 1206. motion direction disambiguation, are encoded only at higher levels in the visual cortical area hierarchy,
 1207. and are absent in V1 (9, 10, 77-81)). Most electrophysiological studies in the behaving primate point to
 1208. the late retroaction in V1 of a top-down signal gated by attention (82-85). They attribute the delay of
 1209. several tens of milliseconds of the change in firing of V1 cells after response onset, to the late action of
 1210. the cortico-cortical feedback (86-90), rather than to the slow horizontal propagation in V1. However,
 1211. puzzlingly enough, axonal feedback transmission from higher areas is 10-100 times faster than intrinsic
 1212. diffusion in V1 (see also (91) for the parallel recruitment of dual lateral-feedback kinetics).

1213. The challenging view presented here is that, as early as V1, horizontal connections play already an
 1214. important role in the early perception of retinal flow and global motion. The visibility and spatial
 1215. spread of their functional dominance in cats & ferrets vs non-human primates (NHP) may reflect
 1216. species-specific differences in retino-cortical magnification factor. Horizontal axon length (4-8 mm) is
 1217. the same across species, but covers up to 8° of visual angle in cat-ferret (cat : (54, 55, 92); ferret : (59)
 1218. whereas it remains within a radius of 1.5 hypercolumn (2-3°) in primates (93), which matches the
 1219. spatial extent of collinear facilitation observed in human psychophysics (42, 94-96).

1220. The multi-stroke AM protocols (“cardinal” and “radial”) were both designed to promote the in-
 1221. phase synchronization of the synaptic impacts produced by the sequential stimulation of each GP

1222. flashed along the motion path with the central feedforward drive (orange arrows in Fig. 1A). Our
 1223. prediction was that this synchronization would be optimized for a flow speed in the range of the
 1224. apparent propagation speed of horizontal connectivity (ASHP in (26) and has been confirmed by the
 1225. speed-dependency tuning study reported here (see Results). However, the variability of the
 1226. intracellular anticipatory Vm profile across cells suggests that other synaptic recruitment paths
 1227. are likely to contribute, in particular the neighbor-to-neighbor links (grey arrows in Fig. 1A). It is thus
 1228. likely that the “horizontal” drive efficiency results from a combination of the asynchronous visual
 1229. activation of two classes of synaptic sources: 1) long-range monosynaptic inputs recruited at different
 1230. eccentricities, whose distributed and delayed impact is integrated in phase by the target cell; 2)
 1231. polysynaptic short-range input, reflecting chains of next-to-next neighbor activation (studied in our
 1232. previous 2-stroke AM (29)). This second effect is amplified by the re-ignition process, imposed at each
 1233. GP locus by the next feedforward input recruited on the apparent motion trajectory. Note that this
 1234. rolling wave effect is not seen for single stroke stimuli, since, otherwise, the spiking discharge field of
 1235. the recorded cell would extend far beyond the spatial region defined by the core thalamo-cortical
 1236. projection.

1237. Since the reverberation delay imposed by cortico-cortical loops is in the order of a few
 1238. milliseconds only (97), it is plausible that most long-range interactions in the primate may operate by
 1239. nested polysynaptic feedback afferents from higher cortical areas operating through chains of
 1240. neighbor-to-neighbor lateral relays, whereas in the cat and ferret, a substantial part would remain
 1241. encapsulated monosynaptically within V1 (7). Our results may provide new insights on the
 1242. evolutionary complexification of cortico-cortical computation. They could also spark interest in AI and
 1243. deep learning in artificial vision, where the diffusion effects of horizontal connectivity in a single V1-
 1244. like terminal layer can be confronted with the backpropagation of “network belief” implemented by
 1245. nested feedback connections in a multi-layer hierarchical cortical-like architecture (98).

1246. **2.2. Dependency on spatiotemporal coherence and visual flow speed**

1247. Since 2-stroke AM provided evidence mostly for subthreshold synaptic amplification (29), we

1248. aimed here at promoting the efficiency of centripetal AM CP-ISO sequences to produce a spiking
 1249. discharge, by increasing the number of elementary strokes in the AM sequence, from 3 to 6 from the
 1250. “cardinal” to the “radial” protocols. In the “radial” protocol, the comparison between FULL-RND,
 1251. SECTOR-RND (data not shown), and SECTOR-CP-ISO conditions demonstrates that the boosting of
 1252. sensory responsiveness grows with the level of spatio-temporal coherence. The speed dependency
 1253. demonstrates unambiguously that the contextual control of the cortical transfer function is maximized
 1254. when a causal coherence is reached, i.e. when the horizontal wave predicts the arrival of the
 1255. feedforward wave.

1256. The optimal range of speed (150-250°/s) reported here contrasts with a recent study of
 1257. anticipatory responses in the fixating monkey, best seen for stimuli cross-oriented to the motion path,
 1258. in continuous slow motion across the RF width axis (6.6°-13.2°/s) (99). The authors propose a complex
 mechanism, based on the interplay of the “feedforward” trace imposed by the continuous motion of
 1259. the stimulus and a medium range isotropic horizontal propagation wave. This activity bump still allows
 1260. a suboptimal slight interaction with the feedforward drive when it propagates faster than the stimulus.
 1261. Their interplay would cause a pre-activation of the cells, facilitating in turn the feedforward
 1262. reactivation. This proposed mechanism is highly dependent on the retino-cortical magnification factor
 1263. and does not account for the global dynamics of the anticipatory wave for distances beyond
 1264. monosynaptic connection lateral extent. The propagation speed across long trajectories (> 3° from the
 1265. Spiking discharge field center), well beyond the spatial extent of monosynaptic links observed in NHP
 1266. (<2°), is indeed ten times slower (≤ 0.02 mm/ms) than the apparent speed of horizontal propagation
 1267. (0.05-0.50 mm/ms; see (26, 32)). The global kinetics is more in line with a slower “rolling wave”
 1268. diffusion mechanism (see also *in vitro* (100)). The speed range of this anticipatory wave reported in
 1269. awake macaque (<15°/s) is lower than in the anesthetized cat area 17 (15-40°/s in (39)), who showed
 1270. that a moving square is more rapidly processed than a flashed one. These different effects share some
 1271. similarities with those reported here, but differ significantly in their speed range (by a 10-20 fold) and
 1272. preferred axial sensitivities (CROSS-parallel vs ISO-Collinear). Furthermore, they do not require

1273. collinearity, an hallmark of horizontally-mediated V1 computation.

1274. **2.3. Binding of global and local features in V1**

1275. The current consensus concerning cortical correlates of low-level perception mixes hierarchical
1276. processing and cortico-cortical recurrency : V1 plays a pivotal role in synchronization dynamics back
1277. and forth with high-order cortical areas (16, 101). Intra-V1 synchronization and inhibitory interactions
1278. are hypothesized to interact through a form of “competitive coding”, before the output is further
1279. processed downstream in the cortical hierarchy. A non-exclusive alternative is that reverberating
1280. activity in V1 already concurs to non-attentive “pop-out” perception. We propose that horizontal
1281. connections, intrinsic to V1, are instrumental to the neural implementation of low-level perceptual
1282. Gestalt laws, in parallel or before information is broadcasted to the mosaic of higher cortical areas.
1283. Our data suggest that, in Gestalt-like configurations, they propagate some kind of “network belief”
1284. (built-up on past activity ignition) to the connex V1 neighborhood, the most likely to be next
1285. stimulated (102).

1286. Remarkably enough, the “prediction” wave, seen for “Surround-Only” AM CP-ISO sequences,
1287. binds local information acquired along the motion path. This observation, although recorded in the
1288. anesthetized brain, globally fits with Bayesian theoretical frameworks, where omission of the next-to-
1289. come stimulus in repetitive and predictive activation sequences unmasks an intracortically generated
1290. “expectation” signal mediated by horizontal connectivity. This finding has to be distinguished from the
1291. classical “predictive coding” schema (103), where what is propagated is the “residual error” from the
1292. expectation generated in higher cortical areas rather than the diffusion of the network belief context
1293. (98). At optimized speed, the self-generated “Surround-Only” wave is shown here to exhibit the same
1294. timing as the FF input onset evoked by the next stimulus to come, had it been presented. More
1295. exploration, outside the scope of this paper, would be needed to test how center-surround interaction
1296. is affected by the contrast (low/high) and the orientation (same/mismatch) of the test Center stimulus,
1297. and how possible sub-linearities can be interpreted in the context of the principle of redundancy
1298. reduction framework (104).

1299. Our results suggest that V1 may solve the motion extrapolation problem just through selective
1300. internal diffusion. Our interpretation is supported by theoretical studies of motion extrapolation
1301. (ability to continue to predict accurately the position/speed of a moving object in the sudden absence
1302. of visual input): Kaplan and colleagues implemented a realistic spiking recurrent neural network
1303. simulation of V1/MT (105), and studied cortical dynamics relaxation, when the coherent motion of a
1304. dot was abruptly interrupted by a “blank” period for three different lateral connectivity distributions
1305. (random, isotropic and anisotropic). The main finding, in agreement with this study, was that
1306. anisotropy was required to allow an efficient diffusion of motion information and achieve accurate
1307. motion/position extrapolation in the absence of FF validation (Fig. 4 in (105)).

1308. **2.4. A neural correlate of perceptual bias in speed estimate for collinear motion**

1309. Our electrophysiological findings constitute a potential correlate, as early as V1, of the human
1310. psychophysical speed-up bias in motion flow integration (47, 76). These previous psychophysical and
1311. computational studies from our lab showed that collinear AM sequences - composed of co-aligned
1312. ISO-Gabor patches along the global motion axis - are perceived by humans as moving “faster” than AM
1313. sequences composed by “parallel” CROSS-oriented elements, of the same exact physical speed. The
1314. speed bias decreased as the angle between the local GP inducer and the global motion axis increased.
1315. This bias was highly dependent of the orientation selectivity of the inducer and disappeared for blobs,
1316. which suggests a cortical origin. All reported features show a close link with the synaptic association
1317. field of V1 neurons (29) and the reported data.

1318. Crucially, the speed, for which the speed-up effect is the strongest in humans, peaks at 64 °/s.
1319. Assuming a parafoveal retino-cortical magnification factor ratio of 3 between human and cat (*human* :
1320. (106); *cat* : (107)), the optimal speed-up range of 40-96°/s seen in human would correspond to 120-
1321. 288°/s in cat, which fits remarkably well the 100-312°/s reported here. The 64°/s optimal velocity for
1322. humans corresponds for the cat to a speed of 192°/s on the retina, and an apparent propagation
1323. speed of 0.19 mm/ms in cortex, in agreement with the inference made from our intracellular

1324. recordings. Most remarkably, the boosting mechanism revealed in this study confirms the prediction
 1325. of an earlier computational model of our laboratory (47), which provided a simple conceptual
 1326. framework where synaptic summation between feedforward and lateral AM inputs results in
 1327. amplification and latency advance in V1 spiking responses.

1328. Our intracellular study allows to go one step beyond this spike-based modeling. In (47), the
 1329. composite synaptic summation is linear and the non-linearity of the functional effect is simply due to
 1330. that of spike initiation. However, the intracellular study of the timing dependency of the association
 1331. process suggests a non-linearity in the interaction process between feedforward (FF) and horizontal
 1332. input, which becomes supra-linear when FF input lagged by more than 5.5 ms the contextual signal
 1333. (Fig. 7 C in (29); see also here Fig. 10, right pane)). It remains plausible that a minimal integration time
 1334. is needed to recruit non-linear voltage-dependent mechanisms recruited by horizontal connectivity,
 1335. such as the persistent sodium current or NMDA receptor activation (25, 108).

1336. 3. Concluding statements

1337. In conclusion, the view presented here differs significantly from classical studies/models of top-
 1338. down gain control of V1 processing which ignore the contribution *per se* of horizontal connectivity (11,
 15, 16) or attribute the late enhancement of visual responses in V1 to the exclusive feedback from
 1339. higher cortical areas (83). We do not argue here against the consensus that top-down signals are
 1340. required, during attentive wakefulness, to express and/or amplify an integrative process intrinsic to V1.
 1341. However, our recent demonstration of a “synaptic association field” in the anesthetized preparation
 1342. demonstrates a preexisting structural bias intrinsic to V1, that could constitute the synaptic footprint
 1343. of the neural architecture needed to implement Gestalt laws (29). This finding is further strengthened
 1344. by a multiscale imaging study (40), suggesting that a critical threshold of spatial summation has to be
 1345. trespassed in order to make these long-range interactions detectable, while temporal synergy
 1346. conditions the effective binding of those spatial interactions (39). A likely interpretation is that some
 1347. kind of resonance regime, such as produced here by the multiple stroke reafferent drive, is needed in

1348. the anesthetized state to propagate at the spiking level a functional bias already present in the
1349. subthreshold impact of horizontal connectivity.

1350. The novel conceptual focus here is on the temporal features of horizontal propagation and on
1351. intra-V1 broadcasting. State-of-the-art modeling generally ignores the propagation distance-
1352. dependent delay component whose impact compromises greatly the analytical solving of mean-field
1353. equations (109); but see (110)). Interestingly, recent large-scale network simulations with
1354. topographically-organized horizontal monosynaptic connectivity and distance-dependent axonal
1355. conduction delays (0.10-0.60 m/s) demonstrates the consistency of spontaneous subthreshold waves
1356. with the asynchronous-irregular regime, defining a sparse-wave regime, more in line with a realistic
1357. view of a functional V1 (36). Although our results interpretation seems in agreement with some of the
1358. computational literature on predictive coding applied to contour-through-motion extrapolation and
1359. trajectory extraction, they still remain to be confronted with alternative models which do not require
1360. propagation of a prediction. Other classes of probabilistic and static models (71) do not depend on
1361. propagation at finite speed and apply primarily to isotropic stimuli which are known to be suboptimal
1362. to activate V1.

1363. Overall, our recordings suggest that fast collinear flow facilitates the refinement of anisotropy
1364. integration, distributed over the mesoscopic representation of trajectories across the “horizontal”
1365. layer plane of V1. The Surround-only CP-ISO anticipatory wave, captured “at the right position, at the
1366. right time” in a subset of our intracellular recordings, is indicative of a progressive topological
1367. refinement of activity diffusion in cortical space. In cat visual cortex, using annular stimuli and voltage
1368. sensitive dye imaging, Chavane et al reported correlates of “filling-in” responses (40), which fit with
1369. our subthreshold membrane potential recordings. Using intrinsic optical imaging (which might reflect
1370. more spiking than subthreshold activity), Chisum et al reported in the anesthetized tree shrew, that
1371. ISO-oriented collinear Gabor arrays flashed simultaneously did enhance locally V1 sensory
1372. responsiveness (111). This latter study, which used a static input pattern of 2 second duration,
1373. activating simultaneously all the Surround sites, detected some activity strengthening in the

1374. areas directly (FF) activated by co-aligned local inducers, but failed to observe any spatial expansion of
 1375. lateral activity in the cortical regions representing stimulus gaps. In contrast, our study predicts that
 1376. the dynamic apparent motion animation of the same array, activating in succession the co-aligned
 1377. local oriented inducers, would generate a continuous anisotropic propagation wave, most visible for
 1378. AM speed faster than 50°/s. This diffusion process would, in turn, fill the gaps between local
 1379. feedforward activation zones and promote the extraction of a motion trajectory riding on an
 1380. expanding collinear contour. Evidence in V1 for an expansive “filling-in” process during apparent
 1381. motion finds some support in fMRI imaging studies in humans (112). It could be tested spatio-
 1382. temporally with more precision in cat and NHP, using voltage sensitive dye imaging and fast AM
 1383. sequences.

1384. Irrespectively of the species-dependency of the visual spatial coverage of horizontal connections
 1385. (7-8° in cats vs 1-2° in NHPs, in spite of similar axonal length), multiple stroke AM sequences appear
 1386. best suited to dynamically recruit overlapping “lateral connectional fields” along the motion trajectory
 1387. (90). The optimal separation in the visual field between the GP inducers might however be still
 1388. species-specific, since the orientation selectivity of the horizontal facilitation process seems best
 1389. prominent when co-stimulating the “Far” surround of GP-driven RFs. This intriguing propagation of
 1390. self-generated and propagated prediction at an early stage of visual cortical processing may underlie a
 1391. more profound functional role. It also suggests a possible interpretation of the peculiar geometry of
 1392. saccadic scanpaths of human observers during the viewing of other human faces. Indeed, Alfred
 1393. Lioukianovitch Yarbus long ago reported a striking similarity between the topographic layout of the
 1394. saccadic scanpaths with the most salient collinear contours outlining the perceptual skeleton of the
 1395. face viewed by the observer ((27, 113, 114); review in (115)).

1396.

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1405. **Abbreviations**

- 1406. AM: Apparent motion
- 1407. ASHP: Apparent Speed of Horizontal Propagation
- 1408. CP: Centripetal
- 1409. CF: Centrifugal
- 1410. CROSS-axis : cross-oriented with the motion axis
- 1411. CROSS-RF : cross-oriented (orthogonal) with the RF orientation preference
- 1412. FF: Feedforward
- 1413. GP: Gabor Patch
- 1414. DN: dense noise
- 1415. ISO-axis: collinear or parallel to the motion axis
- 1416. ISO-RF: collinear or parallel to the RF orientation preference
- 1417. MDF: Minimal Discharge Field
- 1418. NHP: Non-Human Primate
- 1419. RF: Receptive Field
- 1420. RND: Randomized
- 1421. SRF: Subthreshold synaptic Receptive Field
- 1422. SN: sparse noise
- 1423. V1: Area 17 in the cat, Primary Visual Cortex

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- 1425. *The authors declare no competing financial interests.*

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 1434.

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1436. Y.F. conceived of the study.
 1437. Y.F., P.B., X.T., B.LB., C.D., M.P., Y.P. and C.M. designed the experiments.
 1438. P.B., M.P., X.T., C.D. and B.LB. collected the intracellular data.
 1439. B.LB., C.D., X.T. (“radial” protocol) and P.B. (“cardinal” protocol) implemented the data analysis.
 1440. C.D. and M.P. designed the figures.
 1441. Y.F. and B. LB. wrote the manuscript.

A Single Cell

B Population (n=13)

Centripetal

Centrifugal