

Foreword

Neurogeometry and entoptic visions of the functional architecture of the brain

The realization of a special issue on “Neurogeometry and Visual Perception” may be seen as a particular challenge. It may indeed be surprising for a general scientific audience to find out that a Journal specialized in systems neuroscience, such as *The Journal of Physiology (Paris)*, publishes a series of papers focused on mathematical approaches aiming at understanding the brain in the light of abstract and formal geometry. Biologist readers may be shocked at the view of the first analytical equation and the concept of “contact bundle”. Perplexity may invade the mind of theoreticians when forced to dive into the structural and functional diversity of the living brain. Both breeds of potential readers might find the interdisciplinary exercise practiced to the limit of their respective background culture.

Our intention here, with the help of *Jean Petitot* and *Jean Lorenceau* who are the guest-Editors for this special issue, is to go beyond the question marks and eyebrows raised at a first pass, and to take the readers where they would normally not wander, most probably because of cultural habits or prejudice. The aim of our enterprise is to illustrate successful attempts in a theoretical field, such as Geometry, to take advantage of the complexity of brain organization and to open a new explanatory referential. We hope to succeed in showing the efficiency of geometrical tools and concepts in unraveling structural aspects of thought and brain association processes from the sole reading of the relational architecture inside the “black box”.

Computer scientists may be skilled enough to retrieve some of the built-in purposes of computing machines by looking at the wiring diagram of the connection boards and the identity of electronic sub-components, but will remain unable to touch the essence of the software running on the brain-dead machines. One reason for which mathematically based introspection of the inner architecture of the brain might be expected to be more successful, may be that the organizational complexity of neural networks is achieved both through phylogeny and developmental processes: evolution and on-going adaptation result in the constantly updated selection of

highly specific connectivity patterns, relating structural organization and function in a causal manner. In computers, the software has no impact on the hardware structure and activity-dependent regulation is absent, taking away all possibility to the implement functional features in the 3D-layout of the computational unit.

1. Previous steps towards neurogeometry

One of the first examples of the conceptual strength of analogies drawn between geometrical operations and cortical organization can be found in the application of Lie transformation group (L.T.G.) theory to the structural organization of visual cortex by William Hoffman [19,20]: the sensory information processed by visual pathways, and in particular by the occipital primary visual cortex, is in a continual state of flux owing to the motion of our eyes, head and body. The majority of motion cues extracted by the visual system are provided by transformations of the visual referential, by the two-dimensional affine transformation groups described in Lie algebra. A straight edge, for instance, will not be affected by a particular combination of the translation operators. For this reason, these invariant transformations define local symmetries with respect to the corresponding image features, and may correspond to predefined constraints in the wiring of the biological system.

A first postulate in the so-called L.T.G. theory applied to primary visual cortex organization was to suppose that an invariant vector field could be defined on the basis of the functional preference encoded in the firing of cortical cells (given by the orientation and direction of the visual stimulus eliciting the strongest discharge) and the spatial location of their receptive fields in the map formed in the layer plane of the cortical structure (corresponding to the retinotopic projection of the visual field onto cortex). A second hypothesis concerned an embedding of mathematical properties in the detailed morphology of each cortical cell. According to William Hoffman: “the morphology of visual cortical

neurons would be a local phase portrait for Lie operators and their shape (pyramidal vs. stellate, anisotropy of the dendritic field) would describe the orbits left invariant by the operator associated with it". His theory predicted, for instance, that the operators (L_x and L_y) of horizontal and vertical translation groups should be embodied in the superficial layers.

A consequence of the L.T.G. model, observable at the biological level, can be tested by adapting the visual system at an early stage of development to the continuous viewing of vertical and horizontal luminance stripes, which are precisely the orbits of L_x and L_y Lie operators. The physiological and anatomical effects of such restricted exposure during a critical developmental period, as defined by Hubel and Wiesel [22], have been extensively studied (review in [13]). The L.T.G. model predicts an enlargement of superficial layers with an increased proportion of tangential "horizontal" intracortical connections corresponding to the retinotopic projection of the luminance stripes imposed through restricted visual experience. Interestingly, some anatomical data in stripe-reared animals suggested that the dendritic fields of large stellate cells (layer III) and of medium pyramidal cells (with basal fields in layer III and layer IV) become elongated and narrowed in sections tangential to the pial surface, when compared with those measured in normally reared kittens [38]. The anatomical orientation axis of the dendritic arborization in the horizontal cortical layer plane would reflect the topological projections of the experienced stripes, through the interplay of activity-dependent processes. This anatomical bias seemed also correlated to the functional orientation preference expressed in the firing of these cells [2,18]. The interpretation was that the final differentiation of dendritic fields of cortical cells would result, under activity guidance, in the selective stabilization of axons originating from input sources aligned along specific horizontal and vertical axis in the visual field.

2. Mind and world are something of a mutual fit

Although the biological validity of the L.T.G. theory predictions was disputed by physiologists [12] and psychophysicists [8,9,24], this example illustrated the fact that abstract geometrical representations may help in understanding the spatial organization of cortical circuits within the brain. The concept of an inner mapping of the outside world, within the layout of the circuits responsible for its decoding, is somewhat reminiscent of the assertion of a homeomorphic fit between the world and mind by the American psychologist William James [23]: "the faculties of our brain are adapted in advance to the features of the world in which we dwell". Such a view posits that the topological organization of sensory networks and the morphology of their elements may

reflect, at least to a certain degree, constraints in their inner functional organization.

Geometry, in this issue, does not refer to a referential in the outer world independent of the organism under scrutiny, but to the internal topological organization of a part of the brain which processes an organized representation of the sensory world. The claim here is that neurogeometry constrains the physical substrate of the binding architecture in the visual system, and thus corresponds to the morphological embodiment of visual percepts. This view, as detailed in depth in Jean Petitot's chapter, has remarkable implications. The "association field" concept in low-level perception, introduced by psychophysicists [11,32], reflects the perceptual bias that our brain has in grouping local information between distant parts of the visual field as a function of their relative orientation content (the "binding problem" [42]). This global capacity for forming associations, specific to the visual system of humans and higher mammals, stems from the implementation at the biological hardware level (V1 level) of predefined constraints between the coding of the position in space and orientation. The local geometrical properties of the association contours (i.e. their curvature) follows the Gestalt principle of "good continuity" and the geometrical ideality of "line" [26]. Using this approach, it has been shown by several topologists that the organization of the visual cortex orientation map, revealed in the occipital primary visual cortex [5,21], can be seen as a mathematically defined contact fiber bundle ("variété de jet"), resulting from the projection of a 3D-space (cartesian coordinates and orientation) onto a 2D surface (the layer plane of the cortical structure). The implementation of such a projection at the neuronal level posits the existence of multilocal processors, each endowed with a geometrical expertise.

The strength of this theoretical approach is that strong correlates can be found at different levels and scales of integration in the cortical network: (1) at the synaptic level, intracellular studies show that synaptic afferent information originates preferentially from local sources whose receptive fields are aligned with the orientation preference of the postsynaptic cell [6,35]; (2) at the network level, anatomical reconstruction of axonal fields in the superficial layers of the cortex, and imaging of metabolic activity, show that binding operates between cortical iso-orientation domains with collinear preference [7]; (3) at the perceptual level, a collinear configuration of Gabor-oriented elements flashed in rapid succession so that it produces apparent motion, is seen moving "faster" if the motion axis is collinear with the orientation axis of each element, compared to the case where each element orientation is parallel and displaced along a cross-oriented motion axis [14]. The association field can thus be seen as the 2D-imprint of a higher-order geometrical operator and its functional

expression corresponds to the collective recruitment of sets of cortical cells bound selectively by intracortical horizontal connections.

The orientation/direction preference of cortical cells is one obvious suspect. However, cortical cells seem to code a variety of additional features, which raises the question of how many “hidden” dimensions may be mapped and overlaid across the same network. Because of experimental constraints, namely the duration of recording of the same isolated single cell, the basic functional properties of cortical receptive fields are usually established using an input space of sparse dimensions. Electrophysiologists, since the 1950s, have been characterizing receptive fields (considered as the impulse response of the sensory system under study) by mapping the detailed topography of visually evoked “on” and “off” responses evoked by the transient presentation or disappearance of light or dark spots, annuli, contrast edges, bars, flanks, corners, gratings of luminance. Only recently, their probe panoply has extended to include dense noise and natural images. Even when using such a restricted set of test inputs, the firing of cortical cells appears to be optimized by a precise combination of multiple preferred elementary geometrical features. In this regard, the network organization appears as a multiplex of functional sub-networks optimized to detect orientation, direction, spatial phase, center/surround contrast configurations [28]. Thus one cannot discard the possibility that multiple fiber bundles coexist within the same network.

One can conjecture that, in the near future, biologists might be tempted to ask sustained efforts from mathematicians in order to unravel further dimensions hidden in the structure. The anatomical, immunohistochemical and why not genomic description of connectivity patterns associated with regular topologies, labelled differentially through the filter of specific functions (orientation, center-surround interaction, cross-orientation inhibition), may open the possibility to tackle the inverse problem: can we re-deploy the multiple sets of anatomical patterns projected on the same bit of superficial layers of cortex into a higher dimensional space, and identify the new dimensions associated with the fiber bundles, which could serve at an abstract level to a unified representation of the perceived objects?

3. Hallucinations, migraines and inside views of the brain

A second illustration of the potential power of neurogeometry applied to visual perception is the field of visual hallucinations. The simplest version corresponds to the spontaneously experienced or induced vision of illusory light sources spread across the visual field. Phosphenes (from the Greek ethymology *phos*-light/*phainein*-show) were initially thought to originate

from within the eye and correspond to some form of “entophthalmic” vision [29]. Phosphenes were often reported when the subject was exposed in a visual environment deprived of an allocentric referential: this would happen if the subject is immersed in a sea of bright flickering lights [17,33] or kept isolated in dark or uniform environments (devoided of contrast). Similar illusions were reported in unsettled awareness stages, when the subject is waking up or falling asleep, and during near-death experiences [1].

More drastic ways could be used to elicit phosphenes from deeper within the brain. A first approach is to press eyeballs or force the subject to make repetitively convergence eye-movements of unusually large amplitude. Effects of such treatment were already reported before 400 BC and led to the initial consensus that “physical light was produced by the eyeball”, a proposal which persisted into the 18th century [15,16,39]. However, since such manipulations are most successful when performed simultaneously on both eyes, the locus of the illusion is nowadays thought to be cortical. A more stringent approach is to bypass the eye and stimulate the brain electrically. A pioneering attempt was made by placing two electrodes, one in the mouth and the other one attached to the front part of the skull and passing current at a low temporal frequency (similar to the dominant bandwidth of the EEG spectrum (4–50 Hz)). The famous Canadian neurosurgeon Wilder Penfield directly stimulated cortical areas after craniectomy in awake epileptic patients. These patients reported the perception of brief localized flashes when the electrode was positioned in the occipital cortex and more complex geometrical patterns when less posterior cortical regions were stimulated. These latter regions were later identified as secondary and association cortical areas [30].

Hallucination refers to “a false sensory perception in the absence of an actual external stimulus”. Its Latin etymological root refers poetically to prating, dreaming or wandering in mind. This latter analogy may be indeed more profound than it seems. It implies that various mental episodes can induce the vivid report by the conscious subject of activity echoes witnessing the inner architecture of specific regions of the brain. Such is the case during acute episodes of aura migraines [27,34], or after taking hallucinogens such as cannabis, mescaline or psilocybin [36,37]. Migraines are often associated with some form of visual disturbances, auras, which appear as regular patterns expanding across the visual hemi-field, taking the forms of fortifications. Although a first classification of drug-induced hallucinations was proposed as early as the mid-19th century, we had to wait for the work of Heinrich Klüver [25] to find a clinical report of four constant geometrical patterns consistently reported by human subjects: (1) tunnels and funnels; (2) spirals, (3) lattices (honeycombs, triangles); (4) cobwebs. Fig. 1 illustrates some of these remarkable



Fig. 1. *Hallucination patterns from inside the brain.* Top left, binocular deep pressure phosphene [40]. Top right and bottom left, paintings from Indian Mexican Huichol artists made under the influence of a hallucinogenic drug (peyote). Honeycomb pattern of visual field planforms (Bressloff, this issue [4]).

patterns and compares them to paintings from the Huichol Mexican Indian tribe under the influence of a hallucinogenic alkaloid derived from the peyote cactus *Lophophora williamsii*. Such visual imagery is dynamic and the illusory contours usually explode from the center of gaze to the periphery, appearing initially in black and white before bright colors take over, and eventually pulsate and rotate in time as the experience progresses. In most cases the hallucinatory images are seen by both eyes and move with them.

Long before mathematicians, philosophers and psychologists were intrigued by the meaning of hallucinatory form constants. A striking analogy can be drawn by blending the allegory of the cavern by Plato [31] and the perceptual-release theory of hallucinations formulated by the British neurologist Hughlings Jackson in 1931. Let us imagine Socrates facing a glass window carved in the rock of the cavern and being absorbed by the view (through the window) of the outside world without noticing the immediate environment of the cavern-room. Let us also imagine that, behind Socrates, a bright fire burns some way off and projects shadows

of objects within the cavern all over the surrounding walls. Let us consider that the light of the exterior (the sensory input) fades away and that now the window glass reflects the interior of the cavern. The shadows originating from the inner fire (our brain) will be perceived as though they came from outside the window of senses.

Mathematicians in short are proposing a similar view. The theoretical approach developed by Wilson, Ermentrout and Cowan [10,41] was among the first attempts to demonstrate that some periodic patterns, similar in geometry to some of the form constants seen during visual hallucinations, could be mathematically derived from the field equations simulating the interplay of coupled excitation and inhibition in the cortical tissue. The group of Paul Bressloff (this issue) generalized their approach to the generation of both non-contoured and contoured hallucinations. They showed that both the logarithmic nature of the retino-cortical map and the intercolumnar architecture of the occipital primary visual cortex (V1) are sufficient to account for the precise geometry of the constant forms [3,4]. These patterns

emerge when V1's spatially uniform resting activation state becomes unstable, and are "seen" in visual space as the reciprocal-transform of the cortical map activation expressed in retinal coordinates. According to Bressloff, his theory predicts that the V1 network operates in two different dynamical modes, the "Hubel–Wiesel" mode or the "coupled ring" mode between iso-oriented columns, depending on the relative excitability of local excitatory and inhibitory circuits and the global level of excitability. Their analytical approach shows that the mathematically deduced results are sensitive to the detailed specification of the lateral (horizontal) intracortical connectivity. This strongly suggests that the cortical mechanisms that generate geometric visual hallucinations are closely related to those used to process edges, contours, surfaces and textures.

4. Consciousness of the inner brain states

One can expect that mathematician will be tempted to apply similar approaches to higher cortical processing, and the path is half composed for elaborate theories of the neurogeometry of art. In the case of color-contrast and kinetic-illusion based art, Seymour Zeki has already illustrated convincingly the possibility that painters, although following their instinct and inspiration, compose visual patterns that optimally elicit a resonance with the inner structure of their visual system, by promoting the neural activation of color-contrast and motion selective areas [43].

I will leave the words of conclusion to Christopher Tyler [40]: "*Entoptic geometric patterns must be regarded as indicators of some further selective process in the physiological pathway, a kind of functional Golgi stain by which certain neural activities are elevated into consciousness while the majority of possible discharges remain ignored*". Visual cortex does more than mirroring visual experience. It sends back a geometrical construct, the trace of which can be found in the echoes it gives to us in the absence of sensory input, or when the fire of the brain-cavern overwrites the glow of the outer world.

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