Chapter 7
Remarks on Invariance in the Primary Visual Systems of Mammals

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7.1 Introduction

Poincaré observed that the perception of space is based on active movements, and relies on the notions of invariance, covariation between sensors and environment, and active compensation ([179], [180], [181], [182]). The research of Piaget has proved the importance of various kinds of geometrical invariance in cognitive and behaviorial development ([173], [177], [176]). To him intelligence is a form of adaptation, the continuous process of using the environment for learning ([174]). Adaptation is a process that can happen at the scale of evolution, development or functioning. In ecology, or in population biology and genetics, it means the adjustment or change in behavior, physiology, and structure of an organism to become more suited to an environment, thus better fitted to survive and passing their genes on to the next generation (Darwin plus Mendel, [45]). In Neuroscience it often means the decline in the frequency of firing of a neuron in response to constantly applied environmental conditions, or more generally, any change in the relationship between stimulus and response that is induced by the level of stimulus (Laughlin, [121]). Adaptation is an ubiquitous essential property of sensory and motor processing, allowing the living systems to sense and anticipate what is changing in the world ([27]). As we will see, invariance can contribute to adaptation, and adaptation can create new invariance structures. Gibson gave a precise formulation of invariance and adaptation in psychology, with special emphasis on vision ([71], [72], [73], [74]). From the formal point point of view, the mathematical theory of groups, and its many extensions in algebra and analysis (cf. 2.3 below for definitions), offer a clear mathematical basis for discussing the notions of invariance ([84]). About Gibson and symmetry groups, see Shaw, McIntyre, and Mace [202]. For a general discussion of psycho-physics, groups and adaptation, see Shepard 1994 [203]. The link between symmetry, groups, perceptual invariance and *a priori* of the brain was discussed by J.Droulez and myself in [57].

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In the following notes, we give examples of invariance, and of its multiform relation to adaptation, in the mammalian visual systems, in cases where the actions of groups can be made explicit. Most of these examples concern the primary cortical visual system of higher mammals: carnivores, scandentia (three shrew) and primates. The text is assembled from a collection of unpublished studies conducted during the years 2004 to 2012, mainly made in collaboration with students and other researchers in the laboratory LPPA (Collège-de-France, Paris). The emphasis is put on the mathematical equations.

The principle underlying these examples is that neurons and brain areas are better understood by describing their *structure of indifference*, i.e. what they neglect in the world for their function, and their *structure of ambiguity*, i.e. how they create new entities from their inputs, allowing internal transformations. We have proposed that group theory, in particular Galois theory, can be seen as an information theory, in the same manner that probability theory subtends several kind of information theories (Fisher, Shannon, Wiener, Kullback, Kolmogorov). The first mathematical appendix is added to explain this point of view.

In order to modelize invariance and adaptation in one neuron or in a set of neurons, we introduce a *virtual space* (that we propose to consider as a kind of *homology group*, in the mathematical sense, cf. [61]), made by combinations of equivalence classes of possible attractors of responses, modulated by relevant stimuli, for categorization. The symmetry groups and the ambiguity groups are acting on this virtual space (cf. 2.4. and Appendix 1 for the precise definitions). In general this space I corresponds to a dimensional reduction of the input stimuli, it is a skeleton of the rapid internal dynamics. In this model the possible responses (of the neuron or the area) correspond to the coupling of virtual classes with dynamical parameters of neurons or interactive sets of neurons. The space M of these parameters can be seen as an unfolding in the sense of Thom ([212]), which introduces structural stability in the process. It contains intrinsic parameters and preferences of the neurons, in general induced by connectivity or ambient activity. Invariance acts both on I and M. Then, in some cases, adaptation is generated by compensation of transformations in homology by transformations in the unfolding, including bifurcations. We suggest that, in many cases, adaptation is a dynamic on parameters that results from changing the attracting state. In turn this dynamic induces a change in rapid dynamics.

This model permits to use at the same time a notion of receptive field (cf. Marr [137]), with adaptable parameters, and a notion of affordance (Gibson), in the form of invariant categorization, thus we can combine the notions of hierarchical visual fields and the notions of sensori-motor loops for perception and action.

We propose that no meaning can emerge without some kind of invariance: at each step of the neuronal sensory process, the neuronal activity is an act of recognition, which, as every act of knowledge, either explicit or implicit, consists in neglecting most of the individual aspects of the input for selecting the output, combining *a priori* knowledge, novelties and inventions.

The exposition starts with a general introduction to invariance from the perspective of groups an categories. Then we summarize several examples of invariance in the visual system, mainly related to its adaptation to motions. The basic group comes from Galilean relativity, and is implemented in the visuo-vestibular system. However, the evolution of higher mammals, and specially carnivores and primates, used other fundamental groups for vision and visual perception: phase space symmetries (i.e. symplectic transformations), internal affine symmetries of colors, affine and projective symmetries of figures, diffeomorphisms of the visual plane, their extension by gauge transformations for colors, and so on. At the end of visual path, we find in particular the Euclidian geometry realized in abstract spaces, and topology.

In section 2, we insist on the role of eye movements for invariant perception. In section 3, we study affine invariance and adaptation in the color space. In 4.1 we describe models of the transformation from simple cells to complex cells and columns in $V1$, with application to the "energy model". Here we see an intervention of special functions theory. In 4.2 we prove that the principles of invariance and probability explain the geometry of the cortical map of orientations in $V1$. In 4.3 we put forward a probabilistic model of optimal gluing of neuronal activities, with applications to callosal connections and disparity. In 4.4 we study *LGN* and $V1$ in tree shrew, in particular the structure of callosal connections and orientation maps. In this part we give a review of the organization of the visual pathway from the retina to $V1$ through the *LGN* in mammals. In 5.1 we discuss the notion of general covariance in $V1$. In 5.2 we describe the projective invariance of the optic flow, for application to MT, MST. In this example we meet the classical invariant theory of linear group representations. In 5.3 we review geometric cells in the para-hippocampal region. In 5.4 we mention higher invariance in recognition. In 6 we briefly outline the way a topology of information quantities, as developed in collaboration with Pierre Baudot, could go deeper into the mechanisms of adaptation and formation of invariance structure.

The original developments are 1) the formal definition of homology, periods and adaptation, in 2.4; 2) the discussion in 3.2 of the affine structure on colors in *LGN* and $V1$ and the description in 3.4 of color constancy in higher visual areas (inspired from David Philipona and Kevin O'Regan); 3) the computations of non-linearities in complex cells and superficial micro-columns of $V1$, through Abel transforms, in 4.1 (work with Simon Capern and Jacques Droulez); in the same subsection, we introduce of a special class of non-linear pseudo-differential operators for transforming field activities from one brain area to another by taking frequencies in account; 4) the link between probability and invariance in the orientation map of $V1, V2$, in 4.2, implying that the map is a Brownian coefficient of a unitary irreducible representation of the Euclidian group (inspired by F.Wolf, T.Geisel, and D.Barbieri, Giovanna Citti, G.Sanguinetti, Alessandro Sarti); 5) the formulation of the gluing of the two eyes and the two hemispheres by callosal connections, in 4.3 (work with Luc Foubert, Jacques Droulez and Chantal Milleret); 6) the explanation of the impossibility for the tupaia to respect orientation preference in its callosal connection (and the possibility for the cat to do that), in 4.4; 7) the hypothesis of general covariance in the area $V1$, in 5.1; 8) a suggestion for the nature of objects and images

in 5.4, modeled on color constancy and using co-cycles; 9) the perspective offered by information theory, in 6 (joint work with Pierre Baudot); 10) the link between the three roads of information geometry given by Shannon (probabilities), Galois (groups) and Thom (catastrophes) theories, in Appendix 1; 11) the general definition of invariant receptive fields, through coefficients of unitary representations of Lie groups, in Appendix 2.

An excellent reference in Neuroscience more than sufficient for all the applications we will present is the encyclopedia in two volumes, "The visual neuroscience", edited by L.M. Chalupa and J.S. Werner (MIT 2004); we will give in most subsection the related articles in this book, refereed as *TVN* or [44].

7.2 The Notion of Invariance

7.2.1 Mathematical Definition of Invariance

Given a set X (in applications the elements x of X can be things or events) and a set G of partial transformations acting on X (i.e. a set of maps $g : X' \to X$ where X' is a subset of X (in applications these transformations can be permutations but they also can be deformations). We note $x \mapsto g.x$ (or $x.g$) the effect of the map on the elements, and we say that an element x_0 of X is an *invariant point* of the action of G if, for each g acting on x_0 we have $g.x_0 = x_0$ (or $x_0.g = x_0$), i.e. x_0 is a fixed point of the action. When G is stable by composition of transformations, i.e. $g,h \in G \Rightarrow g \circ h \in G$, we assume that for the operation $g(h.x) = (gh).x$ (or $(x.g)h = x.(gh)$ respectively). For $g.x$ we say that we have a *left action* of G, and for $x.g$ we say that we have a *right action*.

We need also the more general notion of *co-variant*: given two sets X and Y and a set G acting by partial transformations of both X and Y, on the left for X and on the right for Y, we say that a function f_0 from X to Y is a *co-variant function* if we have $f_0(g.x) = f_0(x).g$, when both terms are defined. In particular a function $x \mapsto f(x)$ of X to a set Y where the action of G is trivial (i.e. for any $y \in Y$ one has $y.g = y$), is a co-variant if and only if, for any g and x such that $g.x$ is defined, we have $f(g.x) = f(x)$. In this last case we also say that f is an *invariant function*, or simply an *invariant*; in fact it is an invariant point of the natural (right) action of G on functions on X with values in Y: $f^g(x) = f(g.x)$.

Remark that covariance appears as a particular case of invariance when the transformations g of Y are everywhere defined and invertible: denote by g^{-1} the inverse operation of g, and consider the set F of all partially defined applications f from X to Y, with the action of G on F given by $f^g(x) = g^{-1}.f(g.x)$, then f_0 is a co-variant for the actions of G on X and Y if and only if f_0 is an invariant point of the action of G in F.

The main concept underlying invariance study is the concept of *group* G, that is a set equipped with a neutral element e and an internal law $(g,h) \mapsto gh$ satisfying associativity $g(hk) = (gh)k$, neutrality $ge = g = eg$ and invertibility (existence of g^{-1} such that $gg^{-1} = g^{-1}g = e$) (cf. section 2.3). For applications in Physics an

important role is played by the theory of *harmonic analysis*, that is the study of unitary linear representations of groups in Hilbert spaces (cf. Appendix 2). Note that the definition we will suggest for *invariance of a receptive field* is based on coefficients of unitary linear representations of a group, thus belongs to harmonic analysis. However, for most applications in Biology we are forced to restrict the action to a certain subset of G, which relies in general on the notion of *groupuscule* (cf. [34]) or the notion of *category* with inverse of arrows, or *groupoids* ([133]).

The theory of groups was invented by Galois to formalize invariance, symmetry and ambiguity, that arize in the study of algebraic equations (cf. [70], [218]); Klein, Lie and Cartan have shown that all of geometry, with its geometrical transformations and curvature notions, can be understood in this framework. And the notion of groups has been extended by notions from categories, introduced by Eilenberg and Maclane (cf. [133]).

In another direction, the notions of signal analysis, in particular Fourier transform or wavelets transforms, have been extended to non-commutative groups, giving the modern harmonic analysis (cf. [222]).

Note that several authors already insisted that invariance in visual recognition is better understood through general Lie groups theory ([64], [143], cf. [168]).

The theory of groups and that of their representations are recognized as fundamental for the description of physical and chemical systems, from Classical Mechanics to Quantum Field Theory through Quantum Mechanics. In order to be useful in Biology these tools have to be adapted to the proper concepts of Biology, taking into account the discrete nature of neuronal networks, and their inherent variability. In particular, as was noticed by René Thom, the usual assumptions of analyticity are not generally valid in Biology. The study of Vision is an ideal occasion to test and adapt these ideas.

7.2.2 Invariance for Neurons or Brain Areas

Consider a set A of neurons a; the biological function of a neuron a is the transformation of an input into an output, thus the biological function of the set A is a vector of transformations. For instance the output of a *primary visual neuron* a is a function $F_a(I;t)$, where t denotes the time of response and I denotes the past images before t. By an image, here, we simply understand the local field of intensity of light captured in the retina. (For taking color in account, we must add a wavelength content, and I must be a vector.) By a response here, we understand the spiking activity -that is, a numerical function of time. However, in general, to understand the behavior of the neuron a we must also take in account internal parameters (of the neuron or the brain) and other inputs than the image (from other neurons or glial cells). Suppose now that a group G acts on both the collection of input activity and the collection of output activity, we say that the set A is *co-variant* for G if its biological function $in_a \mapsto out_a; a \in A$ is co-variant for the actions of G. Note that in most cases the elements g of G do not respect separately the activities of the units a, but they mix the components of the vector activities.

To be concrete let us give four examples of neuronal invariance in the visual information flow, from the retina to areas at the end of the visual path in the brain: 1) adaptation of light sensors to the intensity: here the transformation g is made by global shift and scaling of the luminosity $I \mapsto (I - I_0)/I_1$, it involves a cascade of chemical and electrical processes modifying the response of ganglion cells (cf. P. Sterling in [44]); 2) view-co-variant recognition: there is a group of permutations g of the cells in $V1$ such that, after any translation and rotation of a visual scene, there is a permutation of the cells in $V1$ that gives a response equivalent to the response for the initial scene (cf. G.C. DeAngelis, A. Anzai in [44]); 3) view-invariant recognition: an individual cell in the human fusiform gyrus can be invariant under the animated deformation of a face which is seen (cf. E.T. Rolls in [44]); 4) direction encoding: in the presubiculum of a rat, a head direction cell a is invariant by translation of the head of the rat to a parallel direction, but the collection A of all head direction cells in the presubiculum is co-variant under the group of rotations of the head in the horizontal plane. In fact the response after a rotation corresponds to a permutation in the population, moreover A is also co-variant for the group of rotations of distant visual cues; in this case all the cells a rotate their preference by the same angle (cf. [234]). In this last example, (that of the head direction cells), we see the interest of considering at least two different groups, one acting on the head, another one acting on the distant visual cues; this multiplicity of frames helps to precise the notions of ego-centric and allo-centric reference frames.

Each neuron, each area, obeys to a first form of invariance, which is defined by all the changes in the world or in the nervous system that have no influence on its function. This invites to consider neurons and their assemblies from the point of view of their *indifference* to the changes in the world. Based on this indifference, neurons and areas can share a co-variance with their inputs, defined by all changes in their function which can compensate changes in the world. This permits to consider neurons and their assemblies as operators detecting certain changes in the world.

However, we will also present a dual point of view, that invariance and covariance are first invented by the brain, from molecules to networks, by creating original *ambiguity* groups in internal spaces. This gives geometrical structures on inner spaces. These two kinds of operations, indifference and ambiguity, can be seen as convergence of invariance and divergence of invariance respectively, as there exist convergence and divergence in neuronal networks connectivity.

A basic example of divergence of invariance is given by *inhibition*: a given input can generate two kinds of answers, one excitatory, another one inhibitory, creating an involution in the brain exchanging excitation and inhibition. Remark that in reality, the symmetry is not exact, in general there is more excitation than inhibition (except some balanced cases), and in some brain systems inhibition largely dominates (as the output of Purkinje cells in the cerebellum), but this symmetry between excitation and inhibition gives a principle of organization, which explains part of the functioning of the brain. For instance see M.M. Slaughter in [44].

A basic example of convergence of invariance is given by the ON-OFF cells in the retina: opening or closing light, which are two different stimuli, generate the same response of the so-called ON-OFF cells. Cf. R. Nelson, H. Kolb in [44].

The groups underlying these two examples are isomorphic to the simplest non-trivial group, with two elements; it is noted $\mathbb{Z}/2\mathbb{Z}$ when considered additively, or $C_2 = \{+1, -1\}$ when considered multiplicatively.

In general the invariance structure is neither pure convergence nor pure divergence; the mixture must be described case by case. For instance global multiplication of intensity of light I by a positive non-zero number λ, has no effect on most ganglion cells, by re-scaling, that is pure convergence; but the same light wavelengths composition can produce different responses of the CC-cells in $V4$, for detecting reflectance of objects; this is a re-construction and constitutes a divergence. Both are called adaptation; changes in the entries are compensated by changes in the analysis to produce efficient signals.

We should note a great similarity between Quantum fields and neuronal functions $F_a(\varphi;t)$, where φ denotes a general field input, not necessarily an image, before the time response t and a denotes a cell in an area A. Each neuron at a given time is a function of an extended function, in the same manner that a state of quantum field is a function of all the classical fields, i.e. it is a *function of functions*. From one area to another, we get an operator transforming these functions of functions into other functions of functions, and symmetry groups act on these operators. In the simplest regime, or in first approximation, the operator appears to be linear. In the same manner interactions between fields are expressed in Quantum Field Theory by a linear operators transforming the states. The coefficients of this operator are the correlations (or amplitudes) between the states, input and output. More generally, considering a set of interacting areas $A_1, ..., A_n$ we can consider the correlation coefficients

$$A(a_1, t_1, a_2, t_2, ..., a_n, t_n) = \langle F_{a_1}(\varphi_1;t_1) F_{a_2}(\varphi_2;t_2) ... F_{a_n}(\varphi_n;t_n) \rangle, \tag{7.1}$$

by taking the average over repetition of the events (cf. [96]).

It is known that the *renormalization group* is a necessary tool for giving a sense to the locality of Quantum objects; according to Wilson and Kadanoff ([235], [235]) this group describes the manner the injection of high momentum and high energy levels at small scales influences the theory at all larger spatial scales. We will see in the examples below that *adaptation* is something comparable: a change of the parameters in the receptive fields that are induced by changing the scale, the frame or the context. This subject is further developed in joint work with Pierre Baudot.

One of the first noticed visual adaptation was the tilt aftereffect of Gibson ([71]): when tilted lines are viewed, even during a short time, then a new set of viewed lines appear tilted on the other side. A long time elapsed till, Dragoi, Schummers, Sur et al. ([56], [201], [200]) showed that in V1, near the pinwheels, there exists a corresponding shift of orientation preference of cells.

Michael A. Webster ([227]) remarks that Gibson himself ceased to accord importance to this effect, because he got more and more interested in natural images. However, later on, researchers got a better understanding of the general role of adaptation, underlying vision and all other sensory modalities, even for natural data.

As other sensory systems, the visual system prepares future actions of the animal depending on the contexts. The paradigm of animal action is locomotion. The primitive function of the visual system is to transform the captured light into information on the situation of the animal in its environment and its future direction of displacement. Note that even protozoa can have eyespots (aggregation of light-sensitive pigments) to help them for swimming. So the visual system completes the vestibular system for sensing and controlling the translations and rotations of the head the world (cf. [24]). This information is combined with all other sensory modalities (in particular proprioceptive) for managing the invariance under the relativity group of the physical laws of movements in Euclidean space. This relativity group was described by Galilée (at the birth of Physics); it was formalized into the Galilean group (cf. J-M. Souriau [207]). The Galilean group has 10 dimensions; it is made by the $6D$ groups of rotations and uniform translations, extended by the $4D$ translations in space-time. Due to the principle of inertia, the last part, the change of origin of the frame, needs vision (or somatic sensation) to be detected. This global invariance is the first basic invariance to be controlled by vision from the point of view of evolution, because it allows the animal to internalize what comes from its action and what comes from the changes in the world. Cf. [11]. Galilean invariance was first implemented in subcortical vestibular and visual systems, for instance in the cerebellum, and it was further elaborated in the cortical system, for instance in the vestibular cortex or the parietal cortex. Note that the divergence in Galilean invariance can sustain what has been named *internal models* (cf. McIntyre, Berthoz and Lacquaniti [140]); a spectacular example is the separation of the gravity vector from the linear acceleration in the vestibular system, which appears in the vestibular cerebellum (cf. [245]).

The linear part of the Galilean group is isomorphic to the Euclidean group of $3D$ rigid motions. Poincaré suggested that the general notion of *object* is issued from the manipulation of rigid bodies, the rigidity property being defined by the possibility to compensate the time evolution of the object by a change of Euclidean frame. For Poincaré this compensation characterizes rigid motions, then the nature of ambient space. This approach was recently developed again by D. Philipona, K. O'Regan, J-P. Nadal et al. in the context of sensory-motor contingence with virtual robotic systems ([171]).

In the primary visual area $V1$, the *simple cells* form a system of co-variants under the $2D+1$ translation of an image (two coordinates for the visual plane and one coordinate for the time), and the *complex cells* have responses that are invariant under small translations (cf. section 4.1 below). This invariance was the reason invoked by Hubel and Wiesel ([88]) to explain the appearance of *complex cells* in $V1$; this produces an information on images that is stable under small displacement. Fourier analysis and its localization by wavelets permit to analyze the receptive fields in $V1$ from the point of view of $2D+1$ translation invariance. However a more complete invariance for all translations is achieved in the infero-temporal region (IT), cf. Rolls et al. [188], [191])

Hubel and Wiesel ([87], [88], [89]) also observed that the neurons in $V1$ of cats and monkeys, have a preferred orientation of stimuli, which is constant in vertical

columns of the cortex and varies continuously along the cortical surface. Thus an action of $2D$ rotations in the visual plane is also implemented in $V1$. From the works of F.Wolf, T.Geisel ([238]), and D.Barbieri, Giovanna Citti, G.Sanguinetti, Alessandro Sarti ([16]), it appears that the organization of orientation maps results from the invariance by the group of $2D$ Euclidean displacements, rotations and translations together (see 4.2 below). In the same manner the *disparity* of binocular cells can be studied from the point of view $3D+1$ invariance (cf. Ohzawa, Freeman [159]).

A further function of the visual system is to document the brain on the content of the environment, from the neighborhood of the body to the far landscape. However this information flow is not a passive registration of photons, it results from an active process. A variety of eye movements (saccades, smooth pursuit, VOR, nystagmus, ...) and internal adaptations (accommodation, efferent copy, ...) helps to stabilize space and objects perception during relative motions. In the following lines we only want to give an idea of the complexity of the brain system (in humans or monkeys) that helps to preserve space invariance during locomotion. We will see that invariance is distributed over many areas, not only visual. As said by Alain Berthoz in [27], this system intertwines motor and sensory information in such a manner that it is preferable to abandon the distinction between them.

The basic compensation movements of the eyes to stabilize the image in the retina when the head is moving, is the vestibulo-ocular reflex (VOR); it is composed of a rotational reflex, the angular VOR (aVOR) and a translational reflex (tVOR). To generate rapid (few *ms*) compensation, the aVOR is organized in the planes of the semi-circular canals, which register rotation acceleration in the inner ear. A wonderful example of adaptation for respecting geometry in space is given by the way flatfishes reorganize the connection from canals to eyes muscles during development ([77]). For aVOR and tVOR a path of three neurons exists in all vertebrates (first order afferent contacting hair cells in the labyrinth, second order neurons in vestibular nuclei, neurons in ocular motor nuclei activating extraocular muscle fibers), but many other brain centers in the brainstem and the cerebellum are used to control and adapt the VOR (cf. [237], [75]). Moreover in natural situation, this reflex must be counteracted by other eyes movements for visual exploration or smooth pursuit or motion anticipation, that involve for instance the saccadic system in the brainstem and the reticulate formation, the superior colliculus (*SC*), the basal ganglia (*BG*), the thalamus, the cerebellum and the neocortex (cf. [27]).

The cerebral network concerned with eye movement control involves a very large part of the brain, for instance in the cortex, it involves FEF (frontal eye field), SEF (supplementary eye field, known for its role in motor programs), $preSEF$ (for motor learning), CEF (for motivation), $MT+, V5$ (visual areas concerned by image movement), PEF (parietal eye field, in particular projecting to FEF), and intraparietal areas IPA (for visuo-spatial integration), but also the dorsolateral prefrontal cortex ($DLPFC$), involved in inhibition of saccades, visual prediction and short term spatial memory, plus several areas involved in visuo-spatial attention (as SMG, SPL). The three areas FEF, PEF and $DLPFC$ have strong projection to the SC, the projection of $DLPFC$ being inhibitory. These areas are interconnected with the

parahippocampal region PHC and the hippocampal formation HF, known to play an important role in spatial memory, in the medium and long term. Cf. the review in [178], and [27], [28]. It is also known that vestibular information reaches PHC and HF ([223]) and the intraparietal areas (VIP in monkeys, IPA in humans) ([250]). Thus gaze behavior during locomotion, naturally influenced by visual and vestibular information, modulates the spatial perception and spatial memory, in particular through the interaction of the cortical network $PEF, FEF, DLPFC$ with PHC, HF. In addition there is a strong interaction of $PEF, FEF, DLPFC$ with the brainstem, SC and other sub-cortical nuclei ($NRTP$, OS,...). Moreover we cannot underestimate the important role of the cortico-cerebellar loops in producing the precise movements of the eyes during locomotion (cf. [12], [60], [51]).

An anticipation of the future visual scene is necessary for stable perception (cf. [65]). It relies on an unconscious visual remapping (made by a subset of the visual neurons) preceding the eye movement. In particular neurons in intra-parietal LIP (for monkeys) or its homolog for humans, have activities modulated by the future visual stimulus; in particular they are known to be informed by afference copy of voluntary eye movements ([244], [149]). Such remapping is also present in FEF, SC, and extra-striate visual cortex. This system is known to be modulated by attention. Studies in human primary visual areas have shown visual remapping in the ipsilateral field (cf. [142]), that is a probable feedback from the parietal cortex (normalized responses in visual areas are as follows: in $hV4$ 71%, $V3A$ 61%, $V3$ 35%, $V2$ 23%, $V1$ 17%). Neurons in $V3, V3A, V4$ react to saccades directed to their RFs (more than 20%, less than 24%), and even in $V1, V2$ (respectively 12% and 14%). The cited authors verified that the remapping effect cannot be explained by saccades effect, or by the apparition of the stimulus, or by the independent conjugation of both. (Note that in $V1$ of macaques, Nakamura and Colby ([151]) found less than one cell over 64 responding to remapping; this can be due to the small size of RFs in $V1$ of macaques, inducing error on the stimulus position, or to the difference between human and monkey for attentional effect.) In $V4$ (for monkeys and humans) there are influences of covert attention and oculomotor information, or stimulation of FEF.

On the interaction of motor and sensory systems in $V1$, we must also cite the experimental use of image movements that mimic the natural eye movements in cats (Baudot et al. [19]): these movements have profound effects on the statistics of individual activity of neurons, they modify the non-linearly in the RFs (mostly spiking) and augment the mutual information with the stimulus. In this case, we see not only compensation for stabilization but also adaptation of the RFs for constructing more visual information.

For all the above matter see the chapter XI in TVN, which contains ten articles on eye movements.

Object perception is the main subject in which ideas of invariance have been applied (cf. Rolls, and Riesenhuber, Poggio in TVN, [44]). We will come back to this vast subject in the last sections.

For a stable perception of space and objects, the visual system must compensate transformations of stimuli. For far space this involves $2D$-affine transformations in

the visual plane. Note that this $2D$-affine invariance is used to explain the duration of hand movement and locomotion [25], [169]). For nearer space $2D$-projective deformation occurs. Certainly the way the sensory-motor system works with this extended affine and projective invariance plays a role in the learning of geometry by children, so useful to act in the world (Piaget). Computer vision has made a great use of affine and projective geometry, see Devernay, Faugeras [54] and Lowe et al. [130], [131].

Koenderink et al. have established that the projective geometry of the visual plane organizes the coherence of figure perception in space; cf. [114], [105], [163], [216]. For instance the Pappus theorem, and the Varignon theorem are implicitly used in perceptual judgments. More generally, pictures deformed by projective transformations are recognized (sometimes with difficulty) as the same picture seen from another place.

In the area MT (or $V5$) of primates neurons are sensitive to stimulus speed with respect to the retina frame. In MT and part of MST (or 19 and 37 Broadmann's areas of humans), the so called complex $MT+$, the geometry of the optic flow is exploited to give knowledge of the eyes (or body) position with respects to objects (cf. [119], [147], [11]). For instance, projective geometry describes the optic flow of one eye that appears when the subject moves in the Euclidean space E and looks at pictures drawn on a fixed plane H in it (cf. section 5.2 below). The vector field on H that describes the apparent movement of fixed points of H in the moving frame of the eye, belongs to the special eight dimensional family of projective vector fields, i.e. the infinitesimal transformations that generate the planar projective transformations. Analysis of the invariant characteristics of the optic flow (the characteristics that cannot be compensated by eye movements with respect to the head) relies on the theory of linear representations of the $3D$ rotation group ([115], [103]).

In the dorsal medial superior temporal area ($MSTd$) there are two types of visually responsive cells: 1) expansion/contraction cells, which selectively respond either to an expansion or to a contraction; and 2) rotation cells, which selectively respond either to a clockwise or to a counterclockwise rotation ([210]).

Neurons in the area MST have responses correlated to speeds with respect to a fixed frame in space, thus they compensate for smooth pursuit of the eye so as to extract higher invariant information from relative information in MT (cf. [92]).

It has been suggested that $V1, V2$ computations involve other Lie groups than the Euclidean group: for instance $4D$ and $6D$ symplectic transformations in the description of the energy flow (cf. [18]), or the group of isometries of the hyperbolic plane for analyzing edges and textures in the model proposed by Chossat and Faugeras ([46]). See Petitot's book [168] for a general discussion.

As we will see in 3.3 below the color space in LGN, and partly in $V1, V2$ and $V4$, offers a good example of invariance constructed by the brain in order to work with frequency of light and physical properties of objects; this invariance relies on affine geometry in nD spaces ($3D$ form most mammals because they are trichromatic).

A main subject in this text will be the *general co-variance* of $V1$: we suggest that in $V1$ local deformations of the images are represented, to sense contours and surfaces in motion. The invariance here relies on feed-forward connections from

LGN, on horizontal connections in $V1$ and on feedback from higher areas. The local deformations generate a group with an infinity of dimensions. However it is better in this case to consider limited distortions, thus the considered transformations are better represented by a category, not a group, which consists of open sets of the visual plane (as objects) and diffeomorphisms from an open set to another one (as morphisms), these diffeomorphisms being sufficiently close to the Identity, to insure that they do not deform too much the objects.

Note that considering categories in order to extend the implication of geometry in perception was suggested long time ago by Piaget ([175]).

7.2.3 Categories and Groups

A nice introduction to categories, functors and their use is [133].

A *category* $\mathscr{C}$ is specified by a set $\mathscr{C}_0$ of *objects* $a,b,c,...$, and for each pair of objects (a,b) a set $\mathscr{C}(a,b)$ of *arrows* $f,g,h,...$, equipped with an operation of composition

$$\mathscr{C}(a,b)\times\mathscr{C}(b,c)\to\mathscr{C}(a,c) \tag{7.2}$$

$$(f,g)\mapsto g\circ f \tag{7.3}$$

which satisfy the two following two axioms:

(i) for each a there is an element e_a in $\mathscr{C}(a,a)$ such that whenever it has a meaning $g\circ e_a = g$ and $e_a\circ f = f$;
(ii) whenever it has a meaning we have $(h\circ g)\circ f = h\circ(g\circ f)$.

An arrow $f\in\mathscr{C}(a,b)$ is noted $f: a\to b$ and is said to go from a to b, the object a being its *source* and the object b being its *target*. Another name for arrow is *morphism*. The axiom (ii) is expressed by saying that composition is an *associative* law. The morphisms e_a are called *identity elements*; the axiom (i) asserts they are *neutral elements* for composition to the right and to the left respectively.

For each category $\mathscr{C}$ we can form the dual category $\mathscr{C}^{op}$: it has the same objects but we decide that any arrow $f: a\to b$ of $\mathscr{C}$ becomes an arrow $f^{op}: b\to a$.

Consider two categories $\mathscr{C},\mathscr{C}'$, by definition, a (covariant) *functor* F is the datum of map $a\mapsto F(a)$ from $\mathscr{C}_0$ to $\mathscr{C}'_0$, and for each pair (a,b) of objects of $\mathscr{C}$, of a map from $\mathscr{C}(a,b)$ to $\mathscr{C}(F(a),F(b))$, -usually denoted $f\mapsto F(f)$- such that whenever possible we have $F(g\circ f) = F(g)\circ F(f)$.
Note that, if F is a functor from $\mathscr{C}$ to $\mathscr{C}'$ and G is a functor from $\mathscr{C}'$ to $\mathscr{C}$", the composite maps form a functor from $\mathscr{C}$ to $\mathscr{C}$". A sub-category $\mathscr{D}$ of a category $\mathscr{C}$ is a category specified by a subset of $\mathscr{C}_0$ and subsets of morphisms, containing the identity elements and closed under composition. The embedding from $\mathscr{D}$ to $\mathscr{C}$ is a functor.

A functor F from $\mathscr{C}^{op}$ to $\mathscr{C}'$ is called a contra-variant functor from $\mathscr{C}$ to $\mathscr{C}'$.

A *natural transformation* T between two functors F,G from $\mathscr{C}$ to $\mathscr{C}'$ is a set of arrows $T(a): F(a)\to G(a)$ defined for each object a of $\mathscr{C}$, satisfying the following

commutativity relation for each morphism $f : a \to b$ in $\mathscr{C}$: $T(b) \circ F(f) = G(f) \circ T(a)$. It is a *natural equivalence* when, for every a, the arrow $T(a)$ is invertible. An *equivalence* between two categories $\mathscr{C}, \mathscr{C}'$ is a pair of functors, F from $\mathscr{C}$ to $\mathscr{C}'$ and G from $\mathscr{C}'$ to $\mathscr{C}$ such that there are natural equivalences T from $F \circ G$ to $Id_{\mathscr{C}}$ and T' from $G \circ F$ to $Id_{\mathscr{C}'}$.

Let $\mathscr{C}, \mathscr{E}$ be two categories, the set of contra-variant functors from $\mathscr{C}$ to $\mathscr{E}$ forms the set of objects of a category whose arrows are the natural transformations. This is named the *topos* of $\mathscr{E}$-valued pre-sheaves on $\mathscr{C}$; we denote it by $\mathscr{T}(\mathscr{C}; \mathscr{E})$. The category $\mathscr{C}$ embeds naturally in this topos, if we associate to a the functor $b \mapsto \mathscr{C}(b, a)$. (In fact the complete notion of topos asks for a Grothendieck topology on a category, and considers *sheaves* (cf. Grothendieck and Verdier, SGA4, [79]); here we considered only the so called discrete topology.)

To any set X we can associate the category $\mathscr{M}(X)$ which has only one object, X itself, and whose morphisms are the maps from X to X; to any vector space V we can associate the sub-category $\mathscr{L}(V)$ with linear mappings as morphisms.

A *left action* of a category $\mathscr{C}$ on a set X is a functor F from $\mathscr{C}$ to the category $\mathscr{M}(X)$; a *linear representation* of $\mathscr{C}$ on a vector space V is a functor F from $\mathscr{C}$ to the category $\mathscr{L}(V)$. A right action is a left action of $\mathscr{C}^{op}$. When nothing is specified an action means a left action.

A *group* G is the set of arrows of a category $\mathscr{C}$ with one and only one object o, such that, for every arrow f there is an arrow g with $f \circ g = g \circ f = e_o$. In this case g is unique (because if g' satisfies the same equations, we have $g' = g' \circ (f \circ g) = (g' \circ f) \circ g = g$), it is called the *inverse* of f and it is written $g = f^{-1}$. It is traditional to identify G with $\mathscr{C}(o, o)$, to forget o and to write $e_o = e$. In general, the composition $g \circ f$ is written as a product gf.

By definition a morphism of a group G in a group G' is a functor from G to G'. It is a map φ from G to G' such that $\varphi(e_G) = e_{G'}$ and such that for any pair g, h of elements of G we have $\varphi(gg') = \varphi(g)\varphi(g')$.

Let H be a subgroup of G, two elements g, g' in G are said to be equivalent to the right modulo H if it exist an element h in H such that $g' = gh$. The set of equivalence classes is denoted by G/H. The group G acts on this set by left multiplication. According to Klein this constitutes the model of a geometry.

A Geometry on a set X is characterized by a group G of transformations of X which acts transitively on points (i.e. for any pair x, x' of elements of X there exists an element g of G such that $x' = g.x$), and a space for this geometry is characterized by a sub-group of this group (Klein, Lie, Cartan), thus we are following the invitation of Llinas and Pellionisz ([166] [167]) to visit the brain as a *geometric machine*. Let us stress that most of the involved geometries are not directly represented in the external world, they act inside the brain on internal spaces, which are in general dynamically distributed over many interacting brain areas.

Let us now set forth a scheme for such internal spaces.

7.2.4 Adaptation and Co-homology

Cf. the appendix 1 for mathematical sources of the definitions below.

Individual neurons, denoted a, have functions $F_a(\varphi;t)$ that transform incoming fields φ into numerical time functions, like electric potential or spiking time sequence or firing rate. In many cases it is possible to give precisions on the manner F_a depends on φ. Inspired by the theory of singularities (Whitney, Milnor, Thom, Arnold, cf. Appendix 1), we assume the existence of three sets M_a, I_a, and E_a, the first one has a structure of smooth manifold, it describes the parameters of dynamics of responses of the cell (and its preferences), the second one is discrete in nature and describes the categorization made by the cell (and circuits around it), in particular in relation with the external world, and the third one describes the internal context (that we consider as a sort of boundary condition). We assume the existence of a function σ which associates to any input field φ and context ε in E_a, an element $\sigma(\varphi,\varepsilon)$ of I_a, called a *vanishing cycle*. This can be seen as a virtual state of the neuron, a virtual attractor of the internal dynamics of the neuron, or a combination of them, affected by signs plus or minus, as could be given by reentries. We also assume the existence of a map $\widetilde{P}$ (named the *period map*) which associates to any μ in M_a a numerical function on I_a, that we name a *co-cycle* (and I_a^* denotes their space). Our first hypothesis on the (biological) functions of the neurons is that F_a factorizes through σ and $\widetilde{P}$, i.e. the equation for F_a as a function on $M_a \times E_a$ is given by

$$F_a(\varphi,\varepsilon,\mu;t) = \widetilde{P}(\mu_t)(\sigma(\varphi,\varepsilon_t)) \tag{7.4}$$

Commentary: each point in M_a represents a possible rapid dynamic of the cell; a point in I_a represents a combination of attractors of the dynamics, a skeleton of the dynamics which can represent memory or/and prediction and thus sustains ambiguity; a point in E_a plays the role of an initial condition for the dynamics. The map σ represents the manner the cell and the circuit around it, in particular feedback loops and reentries, integrate the signal φ with the boundary condition, or context, ε. We can imagine that rapid dynamics happens in a fixed set X_a and that I_a describe combinations of stable attractors in X_a. For μ fixed, the function $\widetilde{P}_\mu$ generalizes the notion of a probability law on the effective attractors. Cf. figure (7.1).

We consider M_a as the unfolding of the dynamics of the cell, in the sense of René Thom [212]. Examples of characters of neurons underlying all the processes in the brain were described by Rodolfo Llinas (cf. [125], [126]). Examples of unfolding for neuronal function were given by Izhikevitch [97]. The categorization process, underlying I_a in our model, is also a subject of study, for instance by Jean-Pierre Nadal et al. ([31]). At the level of evolution M, I, X, E are changed, for instance by coupling several systems. We can suppose that M, when fixed, is universal, in the sense of universal unfolding, which implies structural stability of the system, cf. [212].

For describing the role of invariance (or co-variance) in *cell adaptation*, we assume the existence of a group $\widetilde{G}_a$ which acts on M_a and I_a in such a way that, for any $\mu \in M_a$, $\sigma \in I_a$, $g \in \widetilde{G}_a$, we have

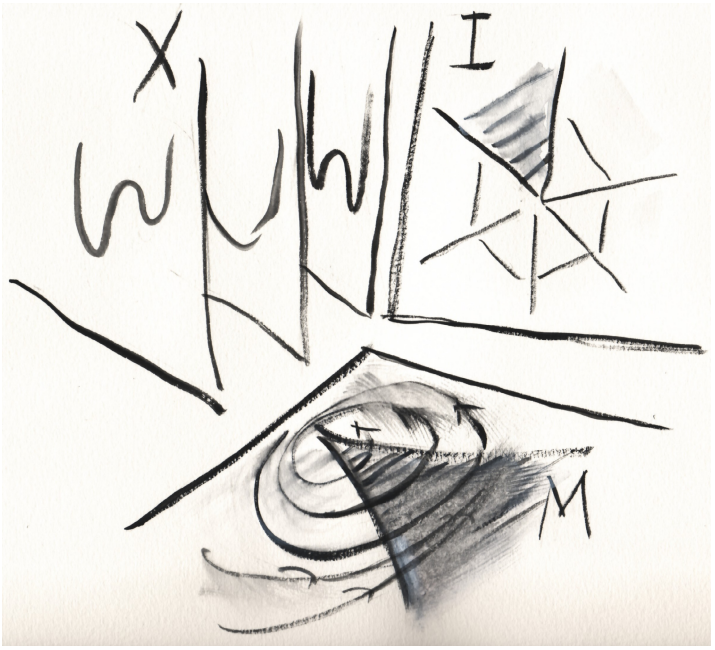


Fig. 7.1 The three dynamical spaces, the internal space X (with its variety of rapid dynamics), the virtual space I (ideal homology, with rigid structures) and the unfolding space M, equipped with a dynamics of adaptation.

$$\widetilde{P}(g.\mu)(\sigma) = \widetilde{P}(\mu)(g.\sigma). \tag{7.5}$$

This relation expresses the possibility to compensate a change of the state σ by a change of the parameter μ. It is more a co-variance than an invariance. In such a way a flow in M changing the parameters of the neurons can compensate a change in the input, the context in E or their interpretations by co-cycles in I.

It is the main suggestion of the present exposition, that it can exist on the unfolding M a dynamic induced by the dynamic in the internal space X of the cell, when expressed by the virtual state in I. This dynamic on M subtends adaptation.

In most interesting examples, the action of $\widetilde{G}_a$ on I_a corresponds to a set of transformations of the input φ and the context ε. But it can happen that some transformations exist only at the level of the cycles σ in I_a. This is the main trend of generation of internal symmetries: new symmetries are generated by ambiguities. We will see examples of both situations.

The action of $\widetilde{G}_a$ on M_a may describe a structural homeostasis, but in general it describes a structural variation, an evolution of the internal system. Moreover, in reality it can happen that a change in context ε or in stimulus φ is not compensated. In general the point μ does'nt change co-variantly, the equation (7.5) expresses a

virtuality, not a necessity. For instance, in $V1$ of cats only the cells at pinwheels follow the ambient change of orientation, not the other cells, cf. [200].
Importantly, a change in M_a can happen without corresponding changes in the context or the stimulus, this change plays the role of an *internal simulation*. This could be the basis of construction of "internal models" (cf. [27]).

Commentary: the origin of symmetries $\widetilde{G}_a$ on I_a is the inherent ambiguity of virtual attractors, they are of Galois type; the existence of its compensatory action on M_a expresses particular cases of dynamics of adaptation. In general these dynamics are slow dynamics that describes the change in the nature of rapid dynamics, rapid reactions. However, adaptation can be very quick, within milliseconds. A wonderful example of that is given by hair cells rapid adaptation in the inner ear ([59], [90], [91]). In the particular case of spontaneous oscillations of hair cells in the bullfrog sacculus the adaptation flow on M has been completely described ([122]).

A guide for understanding this compensation is the dynamics of renormalization in statistical mechanics: in this case the integration of higher frequency band is compensated by a change in Lagrangian for leaving invariant the truncated correlations, i.e. for respecting physics at low frequency scale (large distance). This process generates a semi-group converging to a family of Lagrangian functions that depends on a frequency scale of observation; on this family the change of scale can be expressed by a change in the strengths of interaction. Cf. [96], [235], [236].
There is a parallel between the invariance equation of a cell and the co-variance equation of movement production suggested in [25]. In this paper it was described how movements μ adapt their duration to the action of geometrical transformations g of the space on trajectories σ:

$$(g.\mu)(\sigma) = \mu(g.\sigma), \tag{7.6}$$

meaning that the movement in time $\mu(g.\sigma)$ on the transformed trajectory $g.\sigma$ is given by applying the transformation g to the movement μ on the initial trajectory σ. The groups considered in [25] were the group of affine transformations of the plane, the equi-affine group made by transformations preserving the area, and the Euclidean group. In [24] the Galilean group is considered. Thus invariance in motion production has the same form as invariance in perception; which is not surprising in the above mentioned view that perception is nothing else that overturned action ([27], [126]).

Let A be a brain area. Several cells $a \in A$ form a vector or responses, where groups can act linearly or not. On the union M of all M_a, the union I all I_a and the union E of all E_a, there is a structure of *bundle* over A. A section μ of the bundle $M \to A$ represents a collection of receptive fields in the area A, a section σ of $I \to A$ represent a collection of inputs and a section ε of $E \to A$ a state of contexts as seen by the a in A. However this point of view of bundles and sections is largely misleading, because it neglects the possible interactions in A, the horizontal connections that give structure to an area. What replaces M_a when we go to the area A is a much larger space M_A than the space of sections, in order to take into account the parameters of possible

interactions of the dynamics between the cells a in A. For instance, consider two cells a and b; the dynamical systems on the Cartesian product $X_a \times X_b$ of their internal spaces cannot be reduced to separate dynamics on X_a and X_b, we must consider in addition a variety of couplings. We name the space M_A the parametric space of A. In the case of a finite number of neurons (sic) and finite dimensional spaces M_a the dimension of M_A approaches the product of the dimensions of the M_a, not the sum, as would be the case for the product of the spaces M_a.

However, instead of I_a we consider the product $\mathscr{I}_A$ of all I_a for $a \in A$ and the same for $\mathscr{E}_A$, the product of all E_a for $a \in A$; they are respectively the spaces of sections of the bundles $I \to A$ and $E \to A$. They will play the roles of the spaces of virtual attractors and contexts for the area A; we name them the vanishing homology and the boundary condition respectively.

Moreover we introduce here a vector space V_A to take in account the dimensions of the responses from A (they are the analog of *primitive forms* in Appendix 1). And we assume the existence of a *joint period mapping* which associates to any element μ of M_A and any vector v of V_A a numerical function on the product $\mathscr{I}_A$ of the I_a. Then, using the maps σ_a that associate to each input φ, each cell a and each context ε_a, an element $\sigma_a(\varphi, \varepsilon_a)$ in I_a, we can form the element $\sigma(\varphi, \varepsilon)$ of $\mathscr{I}_A$, and we get the *amplitude of responses*

$$F_v(\varphi, \varepsilon, \mu; t) = \widetilde{P}_v(\mu_t)(\sigma(\varphi, \varepsilon_t)) \tag{7.7}$$

If we assume linearity in σ and v, the applications $\widetilde{P}_v$ define a mapping $\widetilde{P}$ from M_A to $\mathscr{I}_A^* \otimes V_A^*$ (that is the space of co-cycles with multiplicity).

The numerical functions $a \mapsto \widetilde{P}_v((\mu)(a))(\sigma(a)); v \in V_A$, represent the collection of informative outputs of the area A.

If a stimulus φ and a context ε are given, we assume that a well defined cycle σ results, and that we have the response:

$$\rho_v(\mu, \varphi, \varepsilon) = \widetilde{P}_v(\mu)(\sigma(\varphi, \varepsilon)). \tag{7.8}$$

The invariance in the area A is expressed by a group $\widetilde{G}_A$ that acts on the spaces M_A and $\mathscr{I}_A$ and now V_A in such a way that, for any $\mu \in M_A$, $\sigma \in \mathscr{I}_A$, $g \in \widetilde{G}$, $v \in V_A$ we have

$$\widetilde{P}_{g.v}((g.\mu))(\sigma) = \widetilde{P}_v(\mu)(g.\sigma). \tag{7.9}$$

This relation expresses the compensation of a change of the global state σ by a change of the global parameter μ and the vector v, which can correspond to an *adaptation* (in wide sense) at the level of the area A. In particular a flow in M_A, changing the parameters of the joint activity of the neurons a in A, may compensate a change in the joint categorized input.

Take the example of orientation preferences of principal cells in $V1$: this preference is described by an angular coordinate in M_a for each a. After exposition to an environment where orientations are biased with a certain angle α, some cells change their preferred orientation by a turn of $-\alpha$, this modification is understandable from

the action of $\widetilde{G}_A$. According to Dragoi, Schummers, Sur et al. ([56], [201], [200]) this adaptation concerns the neurons near the pinwheels singularities, thus we can consider that a separate subarea corresponds to pinwheel regions, with an invariance structure different from the regular complementary area. However horizontal projections inform the regular area of the changes in pinwheels integration.

If we rotate a given image by a rotation of angle α in the visual plane, there is a shift in activity of the cells, without changing the preferences of these cells, and this shift may produce no effect in certain higher areas; this can be interpreted as the invariance of object after rotation in those areas. This happens for instance in IT (cf. Tanaka et al. [209], [118]).

Remark that an enlargement of the above notions is certainly necessary to describe general covariance under diffeomorphisms; in this case we must replace groups by categories with invertible arrows, i.e. *groupoids*.

We do not pretend that the above model can describe all kinds of adaptation. For instance, at the level of evolution, adaptations invent new structures, or uses old structures for new functions, thus, in our terminology, it appears new spaces M_A, I_A, E_A and groups $\widetilde{G}_A$, and even new areas A (and new animal species). However, every adaptation seems to reflect an internalization of changing rules of interactions between the organism and the external world, motor and sensory, then it could be that an extended model of compensation can describe every adaptation: we should replace the spaces M_A, I_A, E_A by categories of spaces, parametric and virtual, equipped with a functor of period maps, and we should replace the groups $\widetilde{G}_A$ by sets of functors verifying equations of the type of (7.9), prescribing structural variations from reaction dynamics.

7.3 The Affine Space of Color

(The two first subsections below are taken from talks I gave in Collège-de-France, Paris, in 2005, as examples of co-homology operations in perception. The last one in section 4, was inspired by the thesis of David Philipona, January 14 in 2008.)

A full chapter in TVN is dedicated to color; for our discussion, cf. in particular the articles of Webster, Jacobs, Brainard, and De Valois.

7.3.1 The Subjective Manifolds of Color

Cones in the retina react more strongly for certain wavelengths of incoming light. In many mammalian species several kinds of cones exist, allowing the detection of several aspects of the distribution of wavelength. For each category of cones c_i, the detection is fairly well described by a scalar kernel $K_i(\lambda)$, where $\lambda \in \mathbb{R}^*_+$ denotes the wave-length: when a composed light of density $E(\lambda)d\lambda$ (called illuminance), illuminates a surface of reflectance $R(\lambda)$ the model of the response of a cone c_i is given by

$$R_i = \int E(\lambda)R(\lambda)K_i(\lambda)d\lambda. \tag{7.10}$$

This means that its activity is a function of time proportional to R_i.

Note that the response of a cone can only take in account the photons that it absorbs, thus everywhere in the following discussion we must have in mind that the analysis is local in the retina and the efferent areas. In the retina the spatial receptive field of cells that sense color is small (for instance in primate the cones are concentrated in the fovea), but in $V4$ it is large (several tens of degrees).

Remark, dichromatic models take in account the position of the eye with respect to the surface and the angle of incidence of the light beam on the surface, cf. Koenderink's book [113].

In mammals, the number of kinds of cones varies between one and six (sometimes more, but rarely), see Jacobs (in TVN and [98]). In invertebrates (in particular cephalopods) this number can be larger than ten. Nocturnal new-world monkeys for instance have only one. Rodents, ferrets, cats, dogs and tree threw have two types of cones. In general humans and old-world primates have three sorts of cones, they are denoted S, M, L in accord with the wave-length they prefer, short, medium or long respectively. However in humans a non-negligible proportion have only two, and some other (in particular among females) have four sort of cones ([100]). Consequently, in what follows we consider animals having N sorts of cones, not necessarily 3. For the interesting case of Cichlid fishes see [194].

Axiom 1: there exists a minimal number $n \leq N$ such that the set of responses in LGN and V1 can be explained by n functions of the N cone responses.

The number n is called the *chromatic dimension*. The axiom 1 gives a relation of equivalence between light compositions, each equivalence class is called a *color*. No special set of n linear functions is preferable, as soon as they are linearly independent. In particular, the color space is a smooth contractible manifold C of dimension n.

We speak of dichromatic animals when $n = 2$, this is the case for dogs and cats for instance; we speak of trichromatic animals when $n = 3$, this is the case for most old-world primates (or honeybees); and $n = 4$ is tetrachromacy. Tetrachromacy is known to exist for certain primates, in particular for a certain proportion of humans females ([100]).

Let us describe the principle of the experiment which justifies the axiom 1; this principle is attributed to the mathematician Grassmann (1853), which also invented most of the elements of linear algebra (see [116]): A set of m compositions of light $F_i(\lambda); i = 1, ..., m$ is chosen as reference, where m is *a priori* any natural number. Now, to the same subject is presented a light whose composition is a fixed $B(\lambda)$, and at the same time, another light whose composition $A(\lambda)$ is linear in the F_i, i.e.:

$$A(\lambda) = \sum_i a_i F_i(\lambda). \tag{7.11}$$

For instance one light composition is presented at the left eye and the other one at the right eye. Then the coefficients $a_i, i = 1, ..., m$ are varied, and the subject is required to choose the set which gives the better fit between the effects of A and B.

It is not true that positive numbers a_i can always be found for a good fit. First m can be too small, then we augment m until it works. But, in addition, to obtain a good fit, experiment shows that it is necessary to introduce negative combination, i.e. it is necessary to test similarities like

$$B(\lambda) + \sum_i b_i F_i(\lambda) \approx A(\lambda), \tag{7.12}$$

with b_i *a priori* larger than a_i for some index i. Now the first experimental fact is that a good fit always exists. And the second experimental fact is that, when m grows after a certain number n (dependent on the subject and *a priori* on the $F_i; i \in I$), always smaller than N, no gain is obtained and ambiguities appear.

A remarkable fact is that n can be strictly less than N. For instance Jordan et al. 2010 ([100]) have proved than for the women which are known to have at least four sorts of cones, almost all are trichromatic. But they also have proved that tetrachromatic women exist. Very few animal species in the world are proved to have $n \geq 4$: some shallow-water fishes, some birds (pigeons, budgerigars, ...), and insects (butterflies). However, even when $n < N$, the larger is N for a given subject, the better is its discrimination between different colors, at least in some region of C. This was established for monkeys ([192]). On the other side, it is known that subjects having less than the common N sorts of cones have deficits in color discrimination. For instance a non-negligible proportion of humans cannot distinguish red from green, due to the absence of separation between L and M cones. Note this red-green deficit is also a notable characteristic of dog's vision.

In colorimetry, specialists prefer to describe colors by positive coordinates, thus they have chosen (*CIE* 1931), a set of linear combinations E_X, E_Y, E_Z of cone responses (or fundamental colors, like B, G, R for blue, green and red), such that all detectable color have coordinates X, Y, Z which are positives. This is a non-trivial fact, but such a combination exists.

There is a beautiful curved and twisted curve H in C, made of the hues, which represents the set of equivalence classes of pure wave-length spectra $\delta(\lambda = \lambda_0)$, cf. figure (7.2). Another curve G, which looks like an axis, represents light composition without color, i.e. pure luminosity, made only with grays. In the case of dichromacy, the curve H is planar and meets G (cf. Jacobs, study of dog vision.) In the case of trichromacy, the curve H has a convex shape, surrounding G. The closure $\widehat{H}$ of H by a straight segment in C appears in $V1$, not before, and realizes the colors circle of Goethe. The segments issued from the particular white point of G and ending in $\widehat{H}$ are interpreted as saturation of hues, or washed colors. In tetrachromacy or more, the curves H and G (and probably $\widehat{H}$) continue to exist in the hyperspace C, but saturation is multi-dimensional.

The way the space C is defined by similarities (7.12) among all light combinations is typical of homological construction in Mathematics (cf. [61]).

The axiom 1 describes a subjective property, or the final effect in behavior of a neural process which starts in the retina; we will see now one of the basis of this process, at work in the thalamus.

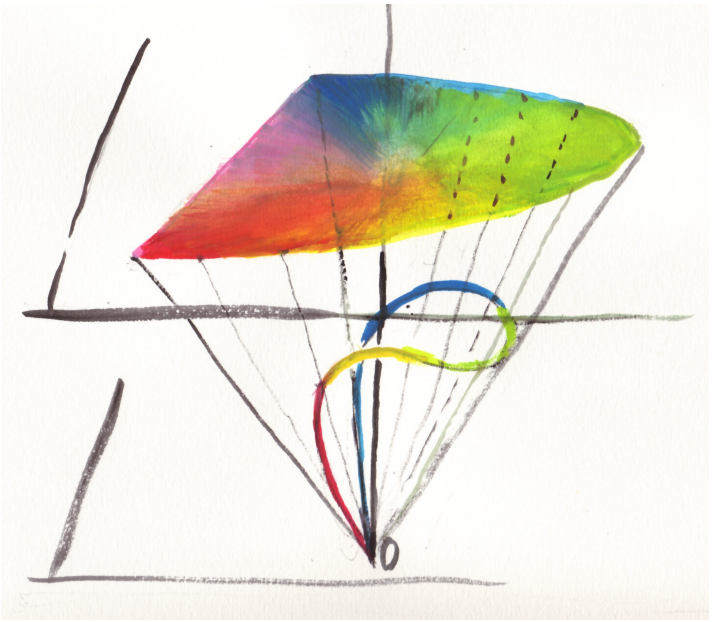


Fig. 7.2 The spectral curve in the color space is the locus generated by light of pure wavelength at fixed energy (cf. [113]). It is curved and twisted and goes through 0. A central projection of this curve gives the CIE triangle of colors; the line of purple joins the two tangent lines that correspond to invisible infrared and ultraviolet respectively.

7.3.2 *An Example of Covariance in the LGN*

Ganglion cells send color information in the LGN by forming linear combinations through excitation and inhibition of the different cones responses.

In case of three kinds of cones, the standard combinations are *brightness* (or luminosity) $S+L+M$, the generator of red-green axis, $L-M$ and the generator of blue-yellow axis: $S-L-M$. We see the use of inhibition for introducing negative coefficients, a proper brain's algebra.

A more exact basis is given by a more complex $3 \times n$ matrix of real numbers. Many different combinations exist for individual ganglion cells, and induce a variety of responses in LGN.

In case of more or less than three cones, it seems that ganglion cells also form n linear combinations of cones. We will consider generic choices of coordinates $(S_1, ..., S_n)$ on C:

$$S_k(ER) = \sum_{i=1}^{n} S_k^i R_i(ER). \tag{7.13}$$

Here E and R are varying illuminance and reflectance respectively, and S_k^i are fixed real numbers.

Axiom 2: In LGN there exists a subset of relay cells $a \in A$, named *affine*, and there exists on C a canonical structure of affine space, such that for any choice of coordinates S_k and any affine cell $a \in A$, the response to incoming light ER is given by

$$A_a(ER) = B_a + \sum_{k=1}^{k=n} A_a^k S_k(ER). \tag{7.14}$$

Remark this axiom does'nt need axiom 1 to be formulated, thus it gives a stronger statement, probably underlying axiom 1, restricted to *LGN*. However apparently the affine structure has a strict sense only in *LGN* and $V1$ or $V2$, because it seems not fully valid for perception. Only the dimension remains for perception, with a more complex geometric structure on the space C, not flat. See [113].
For the affine structure on colors, and more, see [199].

Remark: the coefficients B_a, A_a^k can be modulated by the context and the corticothalamic feed-back. Note that other cells exist in *LGN*, in particular there exists cells which react non-linearly.

This axiom 2 is sustained by wonderful experimental results from the neurophysiology on monkeys (De Valois, Wiesel and Hubbel 1966, Derrington 1984, Lennie, Krauskopf, ...) (cf. in particular [53], [124]): inside the infinite dimensional vector space of local numerical continuous functions of (E,R), the set of possible response functions of the element a in *LGN* forms, in first approximation, a linear subspace of dimension $n+1$.

Definitions: An incident light E generate a marginal distribution $\rho(c)dc$ of colors, having a *mean* $m(\rho)$, which is a point in C, and a *covariance form* $Q(\rho)$, which is a quadratic form on the vector space associated to C (isomorphic to C but centered in $m(\rho)$). In particular the decomposition of *sun light* (or other natural light) introduces a mean point, named 0, corresponding to the *white*, and an Euclidean metric Q_0, characterizing the decomposition of this light at the order two, which we name the *spectrum* of sun light. Choosing this point 0 and this metric Q_0 as references, the space C becomes an *Euclidean vector space* that we denote by E_0. Using this space, which depends on a specific light, we can associate to every point $m(\rho)$ a vector Om and to every quadratic form Q a co-variance operator Σ which is a symmetric endomorphism of E_0. These data became a numerical vector and a symmetric matrix respectively, when we choose in addition special linear coordinates S_k on C.

Note that in general experimenters prefer to introduce coordinates on C, giving to C a linear structure and a basic quadratic metric. This is also a manner to define a structure of Euclidean vector space on C. For example Von Kries suggested to work in the coordinates given by the cone themselves, which gives three preferred axis, and distinguishes the co-variance matrices that are diagonal. However, the only

intrinsic structure of C is its affine structure, not the basis. The structure of the adaptation of affine color cells in *LGN* is precisely based on this fact:

Axiom 3: When, around the receptive field of the cell a, and during a certain interval of time, the ambient color distribution $\rho(\lambda)$ departs from the one of the sun light, we get a mean vector m and a covariance Σ for ρ, then the responses of the cells a are changed by an affine transformation τ of C, i.e. R_a becomes $R_a \circ \tau^{-1}$, to compensate for the change of sun light in ρ.

More precisely, there exists a linear transformation R of E_0 such that Σ is equal to $R^*.R$, and the cell a which had the response $R_a(c)$ (an affine function on C) is transformed into the response $\tau_*(R_a)(c) = R_a(R^{-1}(c-m))$ (another affine function on C). This has the effect to reproduce the world as if it were illuminated by the sun light, at least at the second order of the moments. Then the compensation equation is:

$$R_a(c) = \tau_* R_a(m + Rc). \tag{7.15}$$

Experimental justification of this axiom is given by Stiles 1959 [208], see Webster in *TVN*. Cf. figure (7.3).

For τ negative coefficients are necessary. A remarkable fact, that we suggest to be a common denominator of all co-homological constructions in the brain (in the sense of 2.4), is that *excitation and inhibition* are used carefully to produce the structure (here affine) and its transformations (here affinities) together.

Observe that a transformation of the moments of ρ is not sufficient to define a unique element τ. Many other elements do the job, they differ by the rotations preserving Q_0 if we compose to the left or by the rotations preserving Q if we compose to the right. A natural choice consists in taking for R the root $\sqrt{\Sigma}$, i.e. the unique positive symmetric operator R such that $R_\Sigma^2 = \Sigma$, but we can also compose this R by any rotation S i.e. take $S\sqrt{\Sigma}$. Thus the ambiguity after adaptation is an orthogonal group. There is a possibility to use higher order statistical invariants of ρ to better determine the adaptation, but I know of no experimental basis for that.

We see that color in *LGN* gives a perfect example of the general structure we have introduced for describing invariance: In this case the parametric space M describing the kind of response of affine color cells is the space of affine forms for each cell a, and the affine group G_C acts on M by affine change of variables. We have a special point in M, which is 0, corresponding to the mean information on the world under sun light. The vanishing co-cycles are the colors themselves, they form the space $C = I^*$, and the Galois group G_C acts in the obvious way.

Experiments show the effect of a continuous path of transformation, opposed to sudden changes of color context. Then $\widetilde{P}$ appears.

Remark that most affine cells behave under natural illumination as linear cells, and undergo a translation after adaptation, plus a linear deformation. However several cells (more found in $V1$ but also found in *LGN*) are better explained by absolute values of affine functions on C ([53], [124]), which indicates the pertinence of the n dimensional projective space associated to M.

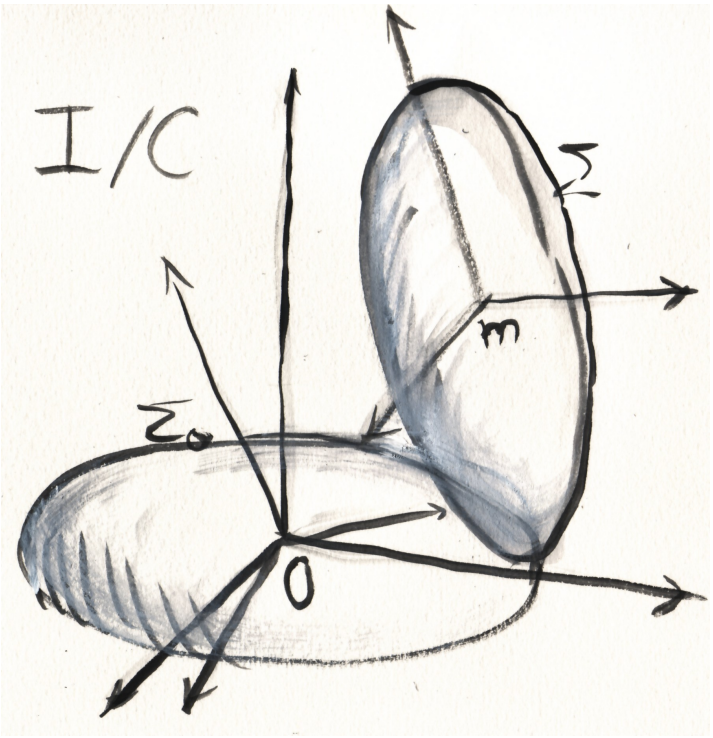


Fig. 7.3 Two ellipsoids for mean and variance of color distribution in the color space I or C; adaptation can deform one into the other, cf. Webster in TVN.

7.3.3 Color in $V1$ and $V2$

The color representation in $V1$ is based on the same principles as in *LGN*, but in $V1$ there is less concentration of cells along special axis (Lennie et al, De Valois et al., cf. [44]). Remarkably the *purple* appears in $V1$, where it is even over-represented for macaques. Cf. [225].

7.3.4 Color Constancy

More advanced areas introduce curvature in the color space, taking in account perception, for instance personal and cultural dimensions. The Riemannian structure on the color space is studied in [199]. In $V4$ context has large influence, cf. Zeki in TVN. The responses become dependent of all other colors. In $V8$ a larger spaces for color is introduced, which represents the distributions of illuminance and reflectance separately.

David Philipona and Kevin O'Regan ([172], [99], [170]) reported a fundamental experimental result for the coding of the relation between illuminance and surfaces reflectance:

Axiom 4: For most homogeneous surface S, there exists a linear operator A^S of C_0 (C pointed in 0), such that for most illuminant $E(\lambda)$, the following relation holds with very good accuracy

$$[SE] = A^S[E], \tag{7.16}$$

where $[E]$ and $[SE]$ denote the equivalence classes in C of the spectrum of a light $E(\lambda)$, and of the same spectrum, once reflected by the surface of reflectance $S(\lambda)$, i.e. $S(\lambda)E(\lambda)$.

The variance accounted by this linear law is larger than 90% for both Munsell chips and natural surfaces ([172]).

Philipona and O'Regan gave a clear justification for this law, following the observations of Judd et al. 1964 [101], and Dixon 1978 [55], that natural illuminants are well explained linearly by three dimensions. Thus, if U denotes the operator sending a basis E_1, E_2, E_3 of this illuminant space to its representation in C_0, and V^S denotes the matrix sending SE_1, S_2, SE_3 in C_0, the operator can be take as

$$A^S = V^S U^{-1}. \tag{7.17}$$

In fact Judd et al. [101] found a basis of spectra made by three or four vectors. Let us observe that even if the illuminants where not well explained by three dimensions, it would be possible to obtain a formula for A^S by taking a pseudo-inverse, as soon as we could assume a linear explanation for E. That is, we consider a generator system $E_1, ..., E_M; M \geq 3$, the operator U_M sending it to C_0 and the operator V_M^S sending $SE_1, ..., SE_M; M \geq 3$ to C_0, and we choose a pseudo-inverse U_M' of U_M (i.e. an operator from C_0 to $\mathbb{R}^M$, such that $U_M' U_M U_M' = U_M'$ and $U_M U_M' U_M = U_M$) and we put

$$A^S = V_M^S U_M'. \tag{7.18}$$

Once normalized, the operator U_M' can be interpreted as an *a priori* probability for each illuminant when the color is given.

Remark that with respect to reflectance, objects appear as transformations in the space C. This invites us to suggest that more generally, *objects*, in the world for a brain, are operators in (co)homology. This suggestion connects a circle of ideas of David Philipona that we discussed during the preparation of his thesis.

Now we will use both the adaptation operator τ and the illumination transforms A^S to propose a formula for constancy.

A surface S is given. Let $E^0(\lambda)$ be the composition of an ambient light, this gives a reflected light $S(\lambda)E^0(\lambda)$ defining a color $[SE^0]$. A new illuminant $E^1(\lambda)$ produces in an analog manner a color $[SE^1]$. We also introduce the pure homology classes $[E^0]$ and $[E^1]$. As we saw before in subsection 3.2, the adaptation from *LGN* to higher areas is realized by a linear operator R_1^0 from C_0 to C_0 such that

$$[E^0] = R_1^0[E^1]. \tag{7.19}$$

Consequently

$$[SE^0] = A^S[E^0] = A^S R_1^0[E^1] = A^S R_1^0 (A^S)^{-1}[SE^1]. \tag{7.20}$$

This gives the following result:

Theorem 3.4.1: The operator $A^S R_1^0 (A^S)^{-1}$ obtained by conjugating the adaptation by the A transform of reflectance compensates the change of color induced by a change of incident light.

A discussion of different matrix models underlying color constancy, along different lines of thought, was made by Maloney-Wandell [135].

Our model is compatible with the result of Yang and Shevell [246], that the presence of two spatially separated illuminants in the scene has the effect of reducing the color constancy. This is due to the fact that in the case of several illuminants, the adaptation R_1^0 cannot be formed.

Considering color distribution in complex natural images, the above formulas can explain only little of the activity of cells and even less of the perception; for that purpose non-linearities and higher correlations in the image have to be involved. These aspects were the main subject of the thesis of P.Baudot (2006) [19], which was the starting point of the research on information geometry and topology he has developed with me, see section 6 below. However, the above linear computations cannot be rejected without care, their existence in simplified situations is not here by hazard. The same is true for the properties of primary visual receptive fields that we will expose now; even if they explain a few percent of the responses of most visual neurons, the fact they exist in simplified contexts is a main pillar for any future theory; see also the section 5.4 on higher invariance.

From the point of view of mathematical education, it is admitted that linear algebra is a good way for beginning. A second step should be differential calculus, as we will encounter in the following section.

7.4 Covariance in $V1$

7.4.1 Simple Cells and Complex Cells

(This chapter is issued from works that grew around the thesis of Simon Capern, Paris VI, September 29 in 2008, in particular it reflects discussions with Simon Capern and Jacques Droulez during ACI NIM (2005-2009).)

Consider a neuron a; its receptive field is better understood as an operator, which transforms a stimulus in a response, respecting causality. The incoming stimulus is represented by a function $\varphi(s,\omega,x)$ where $s \in]-\infty,t]$ represents the time before t, $\omega \in \Omega$ represents chance and $x \in X$ represents variables in the external world; the signal sent to other cells by the neuron a is a function $\psi_a(t,\omega,y)$ of time, chance and other parameters $y \in Y$ describing internal parameters of the brain. This gives a transformation of functions into functions; in general this transformation is

non-linear. The usual way to analyze such a transformation is a Wiener-Volterra expansion:

$$\psi_a(t,y,\omega;\varphi) = f_a(\omega, \sum_{n=0}^{\infty} \psi_{a,n}(t,\omega,y;\varphi)), \tag{7.21}$$

where f_a is a sigmoid function in the second variable and where, for each n,

$$\begin{aligned}\psi_{a,n}(t,\omega,y;\varphi) \\ = \int_{X^n} dx_1...dx_n \int_{\mathbb{R}^n} ds_1...ds_n K_{a,n}(\omega,y,x_1,...,x_n,s_1,...,s_n) \\ \varphi(t-s_1,\omega,x_1)...\varphi(t-s_n,\omega,x_n)\end{aligned} \tag{7.22}$$

for a certain function $K_{a,n}$, named the kernel of order n of the transformation. Cf. [1], DeAngelis and Anzai in [44].

In the simplest model of simple cells in the primary cortical visual system, the function $\varphi_a(s,x)$ represents the normalized intensity of the image at time s and x denotes a point in the visual plane, then the function $\psi_a(t,y;\varphi)$ is the probability of spiking at time t, and the variable y represents the internal context modulating the response, for instance the eyes vergence. In the kernels appear the preferred parameters of the cell, for example a preferred center x_a, a certain disparity vector δ_a depending on the eyes vergence, plus a $2D$ spatial frequency vector ξ_a and a time frequency ω_a. The kernel of order 1 is given by a Gabor wavelet

$$K_1(\omega,y,x,s) = G_a(x-x_a,s)e^{-i(x\xi_a+s\omega_a+\varphi_a)}, \tag{7.23}$$

where G_a localizes $x-x_a$ around 0 and depends on time, giving in particular a delay τ_a where it is maximum and another delay τ'_a where inhibition occurs. In general this distribution is elongated in the direction of frequency vector.

The fact that the Fourier transform of a Gaussian is a Gaussian with inverse variance implies that a strong localization of activity on x_a or t is incompatible with a strong precision on ξ_a or ω_a; thus some cells give good information on the local intensity of the image, while other cells give more information on its frequency structure. Layers IV and V in $V1$ seem to belong to the first type, layers III and II to the second type.

The direction selectivity, i.e. the fact that most cells in $V1$ for cats or monkeys a.s.o. are selective for the direction of the stimulus motion, is well explained by the spatio-temporal structure of the RF, named *inseparability*, i.e. the fact that the vector (ξ,η,ω) and the phase φ form interferences which are not parallel to the time axis, joined to the fact that the time axis is not a principal axis of the RF. Prediction of this model were given for instance by Adelson and Bergen [3], and confirmation is exposed for instance by DeAngelis and Anzai in TVN ([44]). It was also confirmed that the model of linearity followed by non-linearity (i.e. "static non-linearity") explain a non-negligible part of data, see Albrecht, Geisler and Crane in [44].

This receptive field expresses the co-variance for translation in space and time: For simple cells of $V1$, we can start with the group $V_{2,1} = \mathbb{R}^2 \times \mathbb{R}$ of $2D+1$ translations; it is an abelian group and the frequency co-vectors $(\xi_0, \eta_0, \omega_0)$ parametrize the irreducible *unitary* representations of this group. Cf. for instance [222]. Unitarity comes from the reality of the frequency vector. These representations are all of dimension 1, they are given by complex numbers of modulus 1:

$$\chi_0(x,y,t) = e^{i(x.\xi_0 + y.\eta_0 + t.\omega_0)} \tag{7.24}$$

so, they are pure changes of phases.

Let us choose a smooth function K_0 on $V_{2,1}$. By definition an *image* is a distribution I on the space $V_{2,1}$, and a linear simple response of a cell, associated to the kernel K_0, is given by smoothing the real part of an imaginary virtual response represented by

$$E_a(t) = \int e^{-i(x.\xi_0 + y.\eta_0 + s.\omega_0)} K_0(x - x_0, y - y_0, s - t_0) I(x,y,t-s) dxdyds,$$

or equivalently, by using the standard notations,

$$E_a(t) = \langle \overline{\chi_0} \tau_{(x_0,y_0,t_0)} K_0, I_t \rangle = \mathscr{F}(\tau_{(x_0,y_0,t_0)} K_0 . I_t)(\xi_0, \eta_0, \omega_0). \tag{7.25}$$

It represents the element of response at the order one before non-linear rectification. This is the starting point for all what follows: $E_a(t)$ is given by the Fourier transform of $I.K_0$ at the point $(\xi_0, \eta_0, \omega_0)$.

Moreover K_0 localizes images I around the center (x_0, y_0, t_0).

Thus the group of $2D+1$ translations acts on the simple receptive fields by changing the phase, and the visual center.

An important property for Infomax is the *orthogonality of characters* (cf. [222]):

By definition, a character χ on a group G is a morphism form G to the circle group $U(1)$ of complex units. In the case of a finite commutative group, the characters form an orthogonal basis of functions on the group; this is the precise statement of orthogonality. In the present case, because $V_{2,1}$ is an infinite group, then the characters are not square integrable, however something remains of this property of the characters, that is, when we compute the mean over space-time round domain of volume N of scalar products of different characters, we have

$$\frac{1}{N} \int \overline{\chi(x)} \chi'(x) dx \to 0,$$

as N tends to ∞.

Three principles underline the form of the receptive field: 1) Observation of space-time is local and causal; 2) Locality requires commutativity; 3) Elementarity requires irreducibility.

Observe that the same analysis can be applied to all terms of the Wiener-Volterra series, because $I \otimes I, I \otimes I \otimes I, ...$ are distributions on the commutative groups obtained by Cartesian products $V_{2,1}^2, V_{2,1}^3, ...$ respectively, and their irreducible

representations are also given by one dimensional characters; they are parametrized by multi-covectors $(\xi_{\alpha_1}, \eta_{\alpha_1}, \omega_{\alpha_1}, ..., \xi_{\alpha_n}, \eta_{\alpha_n}, \omega_{\alpha_n})$.

Remark: The interpretation of the response formulas by harmonic analysis is not new, it has its origin in Gabor, see Petitot ([168]). Much of the work in this direction were inspired by image analysis, or signal analysis. Several groups have been used, the Heisenberg group ([102]), the group of plane displacements $E(2)$, through its regular representation (Sarti, Petitot, Bressloff, ... cf. [16], and [168]), or the hyperbolic group ([46]) for taking textures into account. The wavelet aspect is fundamental in these studies. It is known that wavelets have much to do with information theory, their efficiency for optimal coding, or maximal compression is well established (or well known); see for instance Atick with Redlich [14], or Dan, Reid, Li Zhaoping, ..., cf. [251]) who explained the mexican hat of Ganglion cells. We should also note that Olshausen and Field [161], [162], Nadal, Parga, Brunel [150] have studied the Infomax principle at natural frequencies. Cf. [1].

In fact a more efficient model of RFs, when compared to experimental data, is given by a finite sum over index $j \in J$ of static-non-linear function u_j (Naka-Rushton, with sign $+$ for excitation and $-$ for inhibition) of kernels centered on points x_j, τ_j, with spatio-temporal extension R_j (non-separable co-variance), evaluated on frequency ξ_j, ω_j with phase φ_j. Cf. [217].

$$R_a(t) = \sum_j \lambda_j u_j(Re[e^{-i\varphi_j} \mathscr{F}(G_j I_t)(\xi_0, \eta_0, \omega_0)]) \tag{7.26}$$

$$u_m(x) = C_0 \frac{x_+^m}{1 + C_\infty x_+^m}; \tag{7.27}$$

However things are not so simple, because experiment also shows that all the parameters in (7.26) (except perhaps x_j, φ_j) depend in a non-linear way of the whole image, through semi-local norms of I and its contrast C. Cf. [42], and Albrecht et al. in [44]:

Lowering the contrast expands spatially the RF and the latency, augments the saturation, and shifts the preferred time frequency to lower values. (Apparently there is no effect on the preferred spatial frequency, and no effect also on the structure of the cortical maps.) There is an advance in spatial phase when contrast augments. But orientation tuning or spatial frequency selectivity vary little with contrast, cf. [204], [8].

Remark that the measured spatial frequency seems higher than the one predicted by Gaussian models, and the same holds for direction selectivity , orientation selectivity and acuity; see Albrecht et al.in [44]. Remark that all these effects can be attributed to interactions, and could theoretically be included in the higher order kernels.

Remark: the shift to the right of time frequency with contrast augmentation can be explained in part by a dilatation of the time difference $t - \tau$: if contrast is multiplied by λ, the transformation of $t - \tau$ into $\lambda^\alpha(t - \tau)$ has the same effect on the response

as the transformation of spatial frequency ω_i into $\lambda^\alpha \omega_i$ joined with a change of φ_i into $(\lambda^\alpha)\varphi_i$. By applying this time dilatation to the windows G_i we also obtain the effect of scaling τ_i and the effect of scaling u_i by a negative power $\lambda^{-\gamma}$ according to Naka-Rushton formula.

The non-linearity u_j, the frequency ξ_j, ω_j and the phase φ_j could also depend non-linearly of time course. For instance there is a general tendency from the first ms to 200ms to shift the cells preference in the direction of higher spatial frequency. There is also a reported shift to higher selectivity with time course which can be explained by the greater expansion of spatial integration as time flows.

A dominant non-linearity comes from the curvature of the *RF*: starting from the linear (or static-non-linear) *RF* we can apply a diffeomorphism of space time (see Dali's watches, and experimental figures of DeAngelis et al., cf. [44]); this introduces shifts in frequency and phase and a change in Naka-Rushton exponents. Moreover this diffeomorphism depends on the contrast in the image over larger and larger domains when time flows. This can be described by the following formula at the order one:

$$R_a^r(t) = \sum_j \lambda_j u_j (Re[e^{-i\varphi_j} \mathscr{F}((G_j I_t) \circ \Phi_j)(\xi_0, \eta_0, \omega_0)]);$$

where Φ_j is a change of space-time variables.

All the above non-linearities describe a particular of adaptation. Thus, we can say that in this case: invariance (given here by translation, and symplectic geometry of light rays acting on the set of irreducible representations of the translations) imposes the form of RF's, and adaptation acts on this set of RF's.

Complex cells can be seen as composition of several simple cells, with comparable frequency preferences but a variety of phases. The same principle can explain in part the response of columns that are seen in optical imaging.

To describe the effect of phase distribution, we consider first the case of *uniform* distribution.

We introduce the hypothesis that among cells in the neighbor of a, we have cells $a', a", ...$ whose subunits possess the same characteristics (G_j, u_j) of a, with the same $(\xi_0, \eta_0, \omega_0)$, but where all angles φ between 0 and 2π are represented with the same probability. References: Pollen and Ronner [183], DeAngelis et al. [49].

The cells form assemblies A with response

$$R_A(t) = \int_0^{2\pi} (u_+(\rho_+(t)\cos(\varphi - \varphi_+(t))) - u_-(\rho_-(t)\cos(\varphi - \varphi_-(t)))d\varphi \quad (7.28)$$

This integral is the difference between two integrals that can be simplified by changes of variables $\varphi \mapsto \varphi - \varphi_+(t)$ and $\varphi \mapsto \varphi - \varphi_-(t)$ respectively, giving

$$R_A(t) = \int_0^{2\pi} (u_+(\rho_+(t)\cos(\varphi))d\varphi - \int_0^{2\pi} u_-(\rho_-(t)\cos(\varphi))d\varphi \quad (7.29)$$

An essential role is played by the transformation $u \mapsto A(u)$, which send the bounded increasing continuous function $u : \mathbb{R} \to [0,\infty[$ to the continuous function $A(u) : [0,\infty[\to [0,\infty[$ defined by the formula:

$$A(u)(\rho) = \int_0^{2\pi} u(\rho\cos\varphi)d\varphi \tag{7.30}$$

This transformation A is named the *Abel transform.*

The integral transform which was originally considered by Abel in 1823 (cf. [2]) is:

$$A_0(u)(\rho) = \int_0^{\rho} \frac{u(r)dr}{\sqrt{\rho^2 - r^2}} \tag{7.31}$$

But A can be easily deduced from A_0 through the change of variable $x = \cos\varphi$, followed by the change of variable $r = \rho x$:

$$\begin{aligned} A(u)(\rho) &= 2\int_{-1}^{1} \frac{u(\rho x)}{\sqrt{1-x^2}}dx \\ &= 2\int_{-\rho}^{\rho} \frac{u(r)}{\sqrt{\rho^2 - r^2}}dr \\ &= 2\int_{0}^{\rho} \frac{u(r)}{\sqrt{\rho^2 - r^2}}dr + 2\int_{0}^{\rho} \frac{u(-r)}{\sqrt{\rho^2 - r^2}}dr \end{aligned}$$

then, denoting $\check{u}(r) = u(-r)$, we find $A(u) = 2A_0(u) + 2A_0(\check{u})$. Moreover in the cases we examine, $u(x)$ is identically zero for $x \leq 0$, and we simply find $A(u) = 2A_0(u)$.

This shows that the usual rectification Re_+ made by simple cells is changed by summation over phases into the modulus non-linearity. Then the most important conclusion for us is:

Assertion: *around the center of its receptive field, the response of a complex cell is invariant by small translations.*

This invariance of complex cells under small translation corresponds to what Hubel and Wiesel had suggested in 1962 ([88]). It is certainly useful in image inspection during micro-saccades of the eyes.

The same result holds for the average of activity in a cortical column, where the phase is uniformly represented.

Remark, in reality the distribution of phases integrated by complex cells is not fully uniform; this gives them a residual phase.

If $u(x) = x_+^{\gamma}$, which annihilates for $x \leq 0$ and coincides with x^{γ} when $x \geq 0$, we have:

$$A(u)(\rho) = [2I_\gamma]\rho_+^{\gamma}, \tag{7.32}$$

where I_γ is given by the Wallis formula:

$$I_\gamma = \int_0^{\frac{\pi}{2}} (\cos\varphi)^\gamma d\varphi = \frac{\sqrt{\pi}}{2} \frac{\Gamma(\frac{1}{2}+\frac{\gamma}{2})}{\Gamma(1+\frac{\gamma}{2})}.$$

Here Γ denotes the Euler function:

$$\Gamma(z) = \int_0^\infty e^{-t} t^{z-1} dt$$

This also permits to obtain $A(u)$ for the most-often-used non-linearities in neurophysiology, introduced by Naka and Rushton (1966):

$$u_m(x) = C_0 \frac{x_+^m}{1 + C_\infty x_+^m}; \tag{7.33}$$

where m is a strictly positive real number. A value which is justified by experiments in V1 is $m = 1,6$ for simple cells, and $m = 2,5$ for complex cells. Thus m is not far from half-integer value, $3/2$ and $5/2$ respectively.

We could also consider the following functions:

$$\tilde{u}_m(x) = C_0 \frac{x_+^m}{(1 + C_1 x_+^2)^{\frac{m}{2}}}; \tag{7.34}$$

their Abel transforms can be computed in terms of usual special functions. Note that for $m > 2$, the functions u_m and $\tilde{u}_m$ differ notably (cf. below).

The function u_m is analytic on $]0,\infty[$ given by a uniformly convergent series on $[0, C_\infty^{-1/m}[$:

$$u_m(x) = C_0 x^m \sum_{k=0}^{\infty} (-1)^k C_\infty^k x^{m(k+1)};$$

thus, using (7.32) with $\gamma = m(k+1)$, we deduce for $\rho \in [0, C_\infty^{-1/m}[$:

$$A(u_m)(\rho) = C_0 \frac{\sqrt{\pi}}{2} \sum_{k=0}^{\infty} (-1)^k C_\infty^k \frac{\Gamma(\frac{1}{2}+\frac{m(k+1)}{2})}{\Gamma(1+\frac{m(k+1)}{2})} \rho^{m(k+1)} \tag{7.35}$$

This expression furnishes a good approximation for $A(u_m)(\rho)$ when ρ is small.

(This function $A(u_m)(\rho)$ is a parent of the generalized hypergeometric series studied by E.M. Wright ([240], [241], [242]) when ρ goes to infinity).

Recall that Γ is log-convex, and satisfies the functional equation $\Gamma(1+x) = x\Gamma(x)$; it follows that the coefficients $\Gamma(\frac{1}{2}+\frac{m(k+1)}{2})/\Gamma(1+\frac{m(k+1)}{2})$ decrease when k increases, they satisfy:

$$(\frac{1}{2} + \frac{m(k+1)}{2})^{-1/2} \leq \frac{\Gamma(\frac{1}{2}+\frac{m(k+1)}{2})}{\Gamma(1+\frac{m(k+1)}{2})} \leq (\frac{m(k+1)}{2})^{-1/2}.$$

From (7.31), we get another formula for $A(u_m)$:

$$A(u_m)(\rho) = 2\rho^m \int_0^1 \frac{t^m}{\sqrt{1-t^2}} \frac{dt}{1+\rho^m t^m} \tag{7.36}$$

We can also start with (7.30), and make the change of variable $t = \tan(\varphi/2)$, this gives:

$$A(u_m)(\rho) = 4C_0\rho^m \int_0^1 \frac{dt}{(1+t^2)} \frac{(1-t^2)^m}{(1+t^2)^m + C_\infty \rho^m (1-t^2)^m} \tag{7.37}$$

This can be integrated with elementary functions when m is integer and with elliptic functions (associated to the lemniscate) when m is half-integer.

For $m = 1$ and $C_\infty \rho < 1$, we pose

$$\kappa(\rho) = \sqrt{\frac{1-C_\infty\rho}{1+C_\infty\rho}},$$

then the transform $f_1 = A_0(u_1)$ is given by:

$$f_1(\rho) = 2\frac{C_0}{C_\infty}[\frac{\pi}{2} - \frac{2\kappa}{1-C_\infty\rho}\arctan(\kappa)]. \tag{7.38}$$

Proof: we consider the function in two variables given by

$$g_1(\rho,\varphi) = \varphi - \frac{2\kappa}{1-C_\infty\rho}\arctan(\kappa\tan(\varphi/2));$$

Its derivative with respect to φ is

$$\begin{aligned}\frac{\partial g_1}{\partial\varphi}(\rho,\varphi) &= 1 - \frac{2\kappa}{1-C_\infty\rho}\frac{\frac{1}{2}(1+(\tan(\varphi/2))^2)}{1+\kappa^2\tan(\varphi/2)^2} \\ &= \frac{1-C_\infty\rho+(1-C_\infty\rho)\kappa^2\tan(\varphi/2)^2 - \kappa^2(1+(\tan(\varphi/2))^2)}{(1-C_\infty\rho)(1+\kappa^2\tan(\varphi/2)^2)}.\end{aligned}$$

By developing the numerator and denominator in function of $C_\infty\rho$ and $\cos(\varphi) = (1-\tan(\varphi/2)^2)/(1+\tan(\varphi/2)^2)$ we get

$$\frac{\partial g_1}{\partial\varphi}(\rho,\varphi) = \frac{C_\infty\rho\cos(\varphi)}{1+C_\infty\rho\cos(\varphi)},$$

therefore

$$g_1(\rho,\varphi) = \int_0^\varphi \frac{C_\infty\rho\cos(\phi)}{1+C_\infty\rho\cos(\phi)}d\phi,$$

and, by making $\varphi = \frac{\pi}{2}$ in this formula we obtain the desired result.

If ρ tends to zero $f_1(\rho)$ also tends to zero. If $C_\infty\rho$ tends to 1, $f_1(\rho)$ tends to $2\frac{C_0}{C_\infty}(\pi/2-\sqrt{2})$.

When $C_\infty\rho > 1$ we define κ as the square root of $(C_\infty\rho-1)/(C_\infty\rho+1)$, a similar computation shows that $f_1 = A_0(u_1)$ is given by

$$f_1(\rho) = 2\frac{C_0}{C_\infty}[\frac{\pi}{2} + \frac{2\kappa}{C_\infty\rho-1}\arg\tanh(\kappa)]. \tag{7.39}$$

Now consider the functions $\tilde{u}_m$. For every positive value of m, we have

$$A(\tilde{u}_m)(\rho) = 2C_0\int_0^1 \frac{\rho^m x^m}{(\sqrt{1-x^2})(1+C_1\rho^2x^2)^{\frac{m}{2}}}dx. \tag{7.40}$$

By putting $t = x^2$ we get

$$A(\tilde{u}_m)(\rho) = C_0\rho^m\int_0^1 t^{\frac{m}{2}-\frac{1}{2}}(1-t)^{-\frac{1}{2}}(1+C_1t\rho^2)^{-\frac{m}{2}}dt \tag{7.41}$$

The hypergeometric function was introduced by Euler (in 1769) by the following integral:

$$F(a,b,c;z) = \frac{\Gamma(c)}{\Gamma(b)\Gamma(c-b)}\int_0^1 t^{b-1}(1-t)^{c-b-1}(1-tz)^{-a}dt. \tag{7.42}$$

This formula has a meaning for any a if we have $Re(c) > 0, Re(b) > 0, z \in]-\infty,+1[$.

If we put $z = -C_1\rho^2, a = m/2, b = m/2+1/2, c = m/2+1$, we have

$$A(\tilde{u}_m)(\rho) = C_0\rho^m\sqrt{\pi}\frac{\Gamma(\frac{m}{2}+\frac{1}{2})}{\Gamma(\frac{m}{2}+1)}F(\frac{m}{2},\frac{m}{2}+\frac{1}{2},\frac{m}{2}+1;-C_1\rho^2). \tag{7.43}$$

The hypergeometric function was studied by Gauss (in 1823) by using series expansions. he found in particular that $A(\tilde{u}_m)$ is given by:

$$A(\tilde{u}_m)(\rho) = C_0\rho^m\frac{\sqrt{\pi}}{\Gamma(\frac{m}{2})}\sum_{k=0}^{\infty}(-1)^k\frac{\Gamma(\frac{m}{2}+k)\Gamma(\frac{m}{2}+\frac{1}{2}+k)}{\Gamma(\frac{m}{2}+1+k)k!}C_1^k\rho^{2k}; \tag{7.44}$$

which converges uniformly for $\rho \in [0, C_1^{-1/2}]$.

By using another formula of Euler we obtain the following formula of $A(\tilde{u}_m)$:

$$A(\tilde{u}_m)(\rho) = C_0C_1^{-\frac{m}{2}}\sqrt{\pi}\frac{\Gamma(\frac{m}{2}+\frac{1}{2})}{\Gamma(\frac{m}{2})}\int_0^{C_1\rho^2} t^{\frac{m}{2}-1}(1+t)^{-\frac{m+1}{2}}dt. \tag{7.45}$$

When m takes integer values, explicit formulas for $A(\tilde{u}_m)$ can be obtained easily from this last formula. For instance if $m = 1$, from (7.45) we get:

$$\frac{d}{d\rho}A(\tilde{u}_1)(\rho) = 2C_0(1+C_1\rho^2)^{-1}$$

Which integrates to

$$A(\tilde{u}_1)(\rho) = \frac{2C_0}{\sqrt{C_1}}\arctan\sqrt{C_1}\rho. \tag{7.46}$$

When ρ tends to zero we verify that $A(\tilde{u}_1)(\rho)$ is equivalent to $2C_0\rho$, and when ρ tends to infinity we see that $A(\tilde{u}_1)(\rho)$ tends to $\pi C_0/\sqrt{C_1}$, which is coherent with the fact that the limit of $\tilde{u}_1(x)$ when x tends to infinity is equal to $C_0/\sqrt{C_1}$.

When $m = 2$, by putting $C_1 = C_\infty$ we obtain $\tilde{u}_2 = u_2$, and in this case the formula (7.45) gives

$$A(u_2)(\rho) = \pi\frac{C_0}{C_1}\int_0^{C_1\rho^2}(1+t)^{-\frac{3}{2}}dt.$$

Which can be computed as

$$A(u_2)(\rho) = \pi\frac{C_0}{C_1}(1-(1+C_1\rho^2)^{-1/2}). \tag{7.47}$$

Let us assume that there is a constant $C > 0$, such that u/C is the repartition function of a real positive random variable X (i.e. u is zero out of $[0,\infty[$, positive, increasing and bounded, and C is the limit of $u(x)$ when x tends to $+\infty$). Then the same is true for $A(u)/C\pi$, it is the repartition function of a real positive random variable R. However, it may happen that X has a finite expectation and R has not, or that X has finite variance and R has not. This is the case in the examples we just saw:

1)If X is uniform in $[0,L]$, the function R has a density equivalent to $C/(L\rho^2)$, when ρ tends to ∞, thus it has no mean value.
2) When $u = u_m$, with $C_0 = C_\infty = 1$ to simplify, we have $u'(x) = mx^{m-1}/(1+x^m)^2$, thus X has a finite mean when $m > 1$ and a finite variance when $m > 2$. However the derivative $A(u)'(\rho)$ is larger than a multiple of ρ^{-m}. For $m = 1$ the derivative is equivalent to $C'\rho^{-2}\ln\rho$, and for $m = 2$ it is equivalent to $C"\rho^{-2}$, (cf. (7.39) and (7.47)). Then for $1 \leq m \leq 2$ the expectation of R est infinite, and for $2 < m \leq 3$, even if the mean of R exists, its variance is infinite.
3) When $u = \tilde{u}_m$, with $C_0 = C_1 = 1$ to simplify, the differences between X and R are even more pronounced: the derivative of u in x is $mx^{m-1}(1+x^2)^{-1-m/2}$, then X possesses a finite mean and an infinite variance. (This makes a deep difference between $\tilde{u}_m$ and u_m pour $m > 2$.) But, from (7.45) we see that the derivative of $A(\tilde{u}_m)$ is of order ρ^{-2} at $+\infty$. Thus R never possesses a finite expectation.
All this can have non-negligible consequences on the kind of integration made by the columns of V1, and even on the integration made by the complex cells when the phase disappears.

Remarks: Abel had defined transformations of functions A_α generalizing $A = A_{1/2}$ for real numbers $\alpha \in]0,1[$:

$$A_\alpha(u)(\rho) = \frac{1}{\Gamma(\alpha)} \int_0^\rho (\rho - t)^{\alpha-1} u(t) dt, \tag{7.48}$$

These operators satisfy:

$$A_\alpha \circ A_{\alpha'} = A_{\alpha+\alpha'}. \tag{7.49}$$

Hardy et Littlewood have proved that, for any $p \in]1, 1/\alpha[$, if we write $q_\alpha = p/(1-\alpha p)$, there exists a constant $C_{\alpha,p}$ such that, for any function u defined on the interval $[0,N]$:

$$\|A_\alpha(u)\|_{q_\alpha} \leq C_{\alpha,p} \|u\|_p \tag{7.50}$$

Under the same hypotheses A_α defines a compact operator from $L^p(0,N)$ to $L^{q_\alpha}(0,N)$. In particular the original Abel transform $A = A_{1/2}$ defines a compact operator from $L^{3/2}(0,N)$ to $L^6(0,N)$.

When $p > 1/\alpha$, the transform A_α becomes compact from $L^p(0,N)$ to the Hölder space $C^{\alpha-1/p}(0,N)$.

In particular $A = A_{1/2}$ defines a compact operator from $L^3(0,N)$ into the space of continuous function $C^0(0,N)$ equipped with the uniform norm.

More generally, the result of push-froward integration by columns in $V1$ is described by summing the activities $R_A(t)$ of (7.29) on sets of cells with several phase distributions. This corresponds to peculiar distributions of the parameters $G_\pm, u_\pm, \xi_0, \eta_0, \omega_0$, given by density functions $D_+(\sigma, m, \xi, \eta, \omega)$ and $D_-(\sigma, m, \xi, \eta, \omega)$. Here we suppose that the various non-linearities are of the Naka-Rushton type u_m (or $\tilde{u_m}$) and the kernels $G_\pm$ mostly vary with the variance σ^2, with comparable center (x_0, y_0); this gives the following formula for the responses in optical imaging:

$$\begin{aligned} R_C(I)(t) = &\int D_+(\sigma, m, \xi, \eta, \omega) d\sigma dm d\xi d\eta d\omega A(u_m)(|\widehat{I_t G_+^\sigma}(\xi, \eta, \omega)|) \\ &- \int D_-(\sigma, m, \xi, \eta, \omega) d\sigma dm d\xi d\eta d\omega A(u_m)(|\widehat{I_t G_-^\sigma}(\xi, \eta, \omega)|). \end{aligned} \tag{7.51}$$

This gives a non-linear operator from tempered distributions I over plane-time to continuous functions on this plane-time, which is a difference between two operators of the following type:

$$\begin{aligned} P(I)(x,y,t) = &\int D(\sigma, m, \xi, \eta, \omega) d\sigma dm d\xi d\eta d\omega \\ &A(u_m)(|\int G_\sigma(X-x, Y-y, s) I(X, Y, t-s) e^{-i(X\xi + Y\eta + s\omega)} dY dY ds|) \end{aligned} \tag{7.52}$$

The preference of the column for an orientation and a spatial frequency corresponds to a particular concentration of the density D in the vector (ξ, η); there also exists concentration for the temporal frequency ω.

It is tempting to suggest that operators from a cortical area Ξ to another one Υ are of the same type, i.e. given by a non-linear pseudo-differential operator.

We could introduce, the places x and y in the area Ξ and Υ respectively, the frequency vectors of spatial activation λ and μ and importantly the time frequencies ν and ω; we would have kernels $D(y,x,\sigma,m,\nu)$ non-necessarily positive, where σ denotes the diffusion factor and m a parameter for non-linearity of functions $f_m : \mathbb{C} \to \mathbb{R}$, in such a way that for any activity $\varphi(x,s)$ in the area Ξ, the impact of φ on the activity in Υ is represented by the formula

$$P(\varphi)(y,t) = \int D(\sigma,m,\lambda,\omega)d\sigma dm d\lambda d\omega \\ f_m(\int G_\sigma(y,x,s)\varphi(x,t-s)e^{-i(x\lambda+s\omega)}dxds) \quad (7.53)$$

This operator has to be composed with an operator of the same type describing the horizontal dynamics in Υ, and a feedback from Υ to Ξ, and so on, so we are face with a graph of propagation. But even this graph is an oversimplification, because quickly a set of areas should be treated as being in interaction, and we come back to an operator from activity in the set of areas to activities in the same set, modulated by external input.

However, we should remark that the dynamics cannot be fully reduced to such a semi-local non-linear pseudo-differential operator, for a more fundamental reason: contextual effects propagate to modify the parameters of the kernels in a non-linear way. The simplest effect is the non-linearity due to contrast: it integrates the contrast by semi-norms in the image, which modify m, σ, saturation and time delays. Thus, at the level of complex operators, adaptation can be represented by a transformation of the density $D(\sigma,m,\lambda,\omega)$.

To conclude this subsection, we come back to the original motivation of the above work on Abel transform, which was the thesis of Simon Capern. We tried to understand the remarkable phenomenon of invariance discovered by Basole, White and Fitzpatrick 2003 ([18]):

Basole et al. observed that several stimuli of different geometric designs, different velocities (in speed and direction), different contrasts produced the same activity of micro-columns in $V1$, as seen by optical imaging. They invoked a motion energy model and suggested that the cortical maps do not represent distinct parameters (position, frequency, orientation, direction) but mixtures of them. However, in his thesis Capern showed numerically that all the results of Basole et al. can be reproduced by the model of columnar responses exposed in this subsection, with m=1.

Note that Mante and Carandini [136] established a similar result without giving explicit formulas. In addition, let us note that these formulas are showing that the results of Basole et al. 2003 are compatible with the existence of geometrically independent maps, but this does'nt prove their independency.

In micro-columns of $V1$ and $V2$ the preferred orientation of neurons do not change, and the same is true of the preferred spatial frequency (cf. [95], [184]), but it seems that the preferred temporal frequency is not organized in the same way

(cf. [109]), consequently the invariance of columns is not for $2D+1$ translations but for $2D$ translations only.

7.4.2 *Orientation Maps, Probability, Co-variance and the Number Pi*

References: Wolf and Geisel ([238], [239]), Kaschube et al. [106], Barbieri, Citti, Sanguinetti, Sarti, 2011 ([16]); Bednar ([20]).

In this third example, we will use Euclidean geometry, probability (bivariate Gaussian fields) and harmonic analysis (which in some sense unifies geometry and probability).

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In $V1$ of all mammals the neurons have preferred orientation (and spatial and temporal frequencies) of stimuli in the visual plane ([87], [88], [89]). In carnivores and primates these preferences are arranged in regular maps along the cortical surface ([30]). Note this is not the case for all species of mammals, for instance rodents, even squirrels which have a fine vision (and a large V1), do not have orientation maps. See [248], [155], [156].

As frequently reminded by Alain Berthoz (cf. [27], [28]), Merleau-Ponty suggested that "To see is to palpate with gaze", thus noticing the parallel between touch and vision, and insisting on the active process that is used in vision as in touch. In the case of the skin of fingers, we see lines in relief (named dermatoglyphes), forming a foliation, which allows for instance to use prints for identification of humans. A biological function of these lines is to help discriminate between touched textures. In exactly the same manner we use small eye displacements (like microsaccades) to vary the cortical input of images and we sense the image with a foliation of inscribed lines in $V1$ (or $V2$), whose tangent vectors are the preferred orientation of the micro-columns. In both cases, fingertips and visual cortex, the singularities are typical singular points of non-oriented fields of straight lines, i.e. either tripods or caps. Cf. figure (7.4).

The singularities of the orientation map are named *pinwheels* (cf. [30], [168]). Around these points there exist polar coordinates (ρ,θ) on the cortical surface such that the preferred orientation is constant when θ is constant.

Following the suggestion of Wolf and Geisel ([238], [239]), we consider that the pinwheels in $V1$ are given by the zeros of a smooth complex function ψ on an Euclidean plane E that represents the visual plane in the cortex.

Remark that orientations (or non-oriented directions) differ from directions of oriented lines in the oriented Euclidean plane, one orientation corresponding to two directions. If we choose in E a given oriented direction δ, the orientations are measured by a real number modulo π and the directions are measured modulo 2π. Thus, given the complex map ψ, we decide that the preferred orientation at the place (x,y) of E is the argument of the complex number $\psi_\omega(x,y)$ divided by two.



Fig. 7.4 Palping/Looking. The curves can represent dermatoglyphics of fingers tips or a map of preferred orientations in $V1$.

The modulus of the function ψ can represent the selectivity level (see for instance [153]).

Taking into account the variability of animals, the variability of their developments and the variability of the map under translation on the cortical surface, we can assume *a priori* that ψ is a random Gaussian field (cf. [4]), of class C^1, on $\mathbb{R}^2$ with values in $\mathbb{C}$. Then the real part $\xi(x,y)$ and the imaginary part $\eta(x,y)$ of $\psi(x,y)$ as well as their derivatives with respect to x and y are continuous Gaussian fields. In accordance with the data and analysis presented by Niebur and Wörgötter, [154], Wolf and Geisel, as Barbieri et al. have assumed that ψ is stationary and isotropic, and has a simple spectral structure.

By the spectral theorem (cf. [4]) we can write the complex field as a sum of random waves:

$$\psi(x,y) = \int d\mu(\overrightarrow{K}) R_\omega(\overrightarrow{K}) e^{i\overrightarrow{K}.\overrightarrow{r}+i\Phi_\omega(\overrightarrow{K})}; \tag{7.54}$$

where $\overrightarrow{r}$ denotes the vector (x,y), where $\overrightarrow{K}$ denotes a dual vector, and μ a positive bounded measure(the spectral measure of ψ), where $\Phi_\omega(\overrightarrow{K})$ denotes a family of random variables with values in $[0,2\pi]$, two by two independent with uniform laws, and with random moduli $R_\omega(\overrightarrow{K})$, of expectation 1.

It is remarkable that this hypothesis alone should be sufficient to estimate the density of pinwheels d_2. Berry and Dennis (2000, [26]), using a Kac-Rice formula (cf. [4]), found that $d_2 = 4\pi/K_2$ where $K_2/2$ is the variance of any one of the derivatives $\xi_x, \xi_y, \eta_x, \eta_y$.

Now, in the particular case of monochromatic waves, i.e. when μ is a uniform probability on the circle Γ_K of fixed radius $K_0 = 2\pi/\Lambda$ centered on 0 in the dual space V^*, Berry and Dennis proved

$$d_2 = \frac{\pi}{\Lambda^2}, \tag{7.55}$$

This is a consequence of the relation $K_2 = K_0^2$.

Note that a similar result was written as soon as 1998 in the supplementary document of [238], but a proof appeared in [239] after [26].

Remarkably this formula corresponds to the spectacular experimental results of Kaschube et al. ([106]) (cf. also the discussion in Science 2012).

The fact that ψ is monochromatic is essential to get π. It is also probably essential for defining a precise scale in the map.

We should also remark that the monochromaticity could also come from constraints on the spontaneous activity during development, having fixed wave length in each brain region dependent on the wiring. Note that the scale is different for $V1$ and $V2$, and depends on the animal studied ([106]).

Consequently we get the following statement:

Proposition 4.2.1: The density π of the pinwheels with respect to the scale Λ of approximate translation invariance, that is experimentally observed by Kaschube et al., is a corollary of the three hypotheses: 1) the fact that the map comes from the argument of a Gaussian field, 2) the invariance of the probabilistic law of the field by Euclidean displacements, 3) the monochromaticity.

Note that Niebur and Worgotter (1994, [154]) gave arguments for the concentration of the spectral measure on an annulus, that were based on an hypothesis of *local correlation*. When the field is not purely monochromatic the density becomes lower than π ([238]).

Barbieri, Citti, Sanguinetti and Sarti ([16]) have suggested that the formula for ψ, in particular the monochromaticity, should be justified by a principle of minimization of uncertainty for two operators analog to conjugate observable quantities in Quantum Mechanics. This principle expresses the fact that the orientation map is optimal for discriminating between two rigid motions; thus it is closely related to Euclidean invariance.

We can say that in this case adaptation is the adaptation of the cortical map for maximal invariance and information, and that it is realized at the scale of evolution, probably using development scale for complete installation (cf. [20]).

Let us give now a presentation of this work of Barbieri, Citti, Sanguinetti and Sarti:

We start with the structure of invariance; thus we consider the natural action of $E(2)$ on the Hilbert space of L^2 complex functions on the plane $\mathbb{R}^2$. Then we choose

an irreducible factor H of this representation ([222]). Note that this irreducibility will appear later as the origin of the monochromaticity. The elements ψ of H give do not give probability densities on the plane; in this case they give probability laws on the momentum space, after Fourier transform. This is analogous to what happens with the representation of translations where pure waves are localized in frequency, not in space. However the unitarity of the representation of $E(2)$ in H allows for correlation computations: If Y is an Hermitian endomorphism of H, i.e. a real observable, the *mean* of Y in the state ψ is well defined as $\mu = \langle \psi | Y\psi \rangle$, and the variance of Y in the state ψ is well defined by

$$\sigma^2 = \|(Y-\mu)\psi\|^2. \tag{7.56}$$

The uncertainty principle in this framework is a theorem (not very difficult to prove, see [48], [195]) that states that, if X,Y are two observables, and if $[X,Y]$ denotes as usual their commutator $X\circ Y - Y\circ X$, we have

$$\sigma(X)\sigma(Y) \geq \frac{1}{2}\sigma^2([X,Y]). \tag{7.57}$$

Moreover this inequality becomes an equality if and only if there exists a real number λ such that

$$(Y-\mu(Y))\psi = i\lambda(X-\mu(X))\psi. \tag{7.58}$$

Let Y_1 the infinitesimal operator associated to the translation in the y direction, and Y_2 the infinitesimal operator associated to the rotation around $(0,0)$; we denote by $\widehat{\psi}$ the Fourier transform of ψ and by $\widehat{Y_1}, \widehat{Y_2}$ the operators conjugated by the Fourier transformation. Then the uncertainty principle implies that ψ gives the minimum of the product of variances of Y_1 and Y_2 in state ψ, if and only if there exists a real constant λ and a complex constant ζ, such that $\widehat{\psi}$ satisfies:

$$(\widehat{Y_2} - i\lambda\widehat{Y_1})\widehat{\psi} = \zeta\widehat{\psi} \tag{7.59}$$

which in our case, is equivalent to the differential equation:

$$\frac{\partial\widehat{\psi}}{\partial\theta} - i\lambda(iK\sin\theta)\widehat{\psi} = \zeta\widehat{\psi}, \tag{7.60}$$

where the vector $\overrightarrow{K}$ in the dual of $\mathbb{R}^2$ is described in polar coordinates $K\exp(i\theta)$. We consider this equation on the universal covering of the dual plane minus the origin in the usual plane of Cartesian coordinates K,θ. From the Cauchy theorem in distributions spaces we get the general solution depending on an arbitrary distribution $C(K)$:

$$\widehat{u}_{(\lambda,\zeta)}(R,\theta) = C(K)e^{\lambda K\cos\theta + \zeta\theta}. \tag{7.61}$$

But u must be periodic in θ so ζ should be written $i.n$ with $n\in\mathbb{Z}$. Thus the solution is

$$\widehat{u}_n(R,\theta) = C(K)e^{\lambda K\cos\theta + in\theta}. \tag{7.62}$$

From harmonic analysis, $C(K)$ must be a bounded measure, otherwise ψ cannot belong to a factor of the standard representation on the plane.

But the irreducibility of H implies that $C(K) = \delta(K = K_0)$, cf. [222]. This concentration of $C(K)$ is equivalent to the monochromaticity of u_n.

If we replace the operators Y_1, Y_2 by another infinitesimal translation and another rotation respectively we obtain in place of u_n the function

$$u_n(x,y;\alpha,a,b) = \int_0^{2\pi} d\theta e^{\lambda K\cos(\theta-\alpha)-in(\theta-\alpha)} e^{iAK\cos(\theta-\phi)} e^{irK\cos(\theta-\varphi)}. \quad (7.63)$$

adapted to the direction $\exp(i\alpha)$ and the rotation around $\overrightarrow{A} = (a,b) = A\exp(i\phi)$, i.e. the change of variables transforming z into $a + ib + z\exp(i\alpha)$.

Now we should realize that there is no deterministic function ψ which is invariant by displacement and which is at the same time optimal for discrimination between translation and rotation. However, as we will see, if we look for a random field with these properties there do exist solutions. In particular there are solutions obtained by summing functions u_n over an infinity of centers and phases:

Let us take a sum of an infinite number of independent random functions $u_n(x,y;\alpha,a,b)$ associated to random vectors $\overrightarrow{A}_k(\omega)$. After integration over α, this gives:

$$\Psi_n(x,y;\omega) = \sum_k F_n(K,k) \int d\theta e^{irK\cos(\theta-\varphi)-iA_k(\omega)K\cos(\theta-\phi_k(\omega))}. \quad (7.64)$$

If we choose the $\overrightarrow{A}_k(\omega)$ to be independent uniformly distributed in the plane and the series $F_n(K,k)$ to be in l^2, the central limit theorem implies the existence of a constant C_n such that the renormalized sum, obtained by dividing F_n by C_n, converges to a Gaussian random field of class C^1, which is stationary and isotropic, then we can apply the results of Berry and Dennis on d_2.

Remark: we could as well take a random sum

$$\Psi_n(x,y;\omega) = \sum_k C_n F_n(K,k) \int d\theta e^{\lambda_k K\cos(\theta-\alpha_k(\omega)} e^{irK\cos(\theta-\varphi)-iA_k(\omega)K\cos(\theta-\phi_k(\omega))}, \quad (7.65)$$

where the α_k are uniformly distributed with values in $[0, 2\pi]$.

Now consider the irreducible unitary representation associated to the number K; it is given by:

$$T_K(\alpha,a,b)(\widehat{u})(\theta) = e^{iAK\cos(\theta-\phi)}\widehat{u}(\theta-\alpha); \quad (7.66)$$

where as before $a + ib = A\exp(i\phi)$ (cf. [222], see Appendix 2).

If v_1, v_2 are two square integrable functions on the unit circle, the associated coefficient is

$$\langle v_1 | T_K(\alpha,a,b) v_2\rangle = \int_0^{2\pi} d\theta v_1(\theta) e^{iAK\cos(\theta-\phi)} v_2(\theta-\alpha). \quad (7.67)$$

Thus $u_n(x,y;\alpha,a,b)$ is the coefficient of T_K associated to $v_1(\theta) = \exp(irK\cos(\theta - \varphi))$ and $v_2(\theta) = \exp(\lambda K\cos\theta - in\theta)$. The function v_2 obtained when $n = 0$ is the Von-Mises density $v(\theta) = \exp(\lambda K\cos\theta)$.
The final function of the Barbieri et al. model is also a coefficient of T_K:

$$\Psi_n(x,y;\omega) = \langle C_n(K)T_K(0;x,y)V(\omega)\rangle; \tag{7.68}$$

The Gaussian field itself is given by the stochastic integral:

$$\Phi(re^{i\varphi};\omega) = \frac{1}{2\pi}\int_0^{2\pi} C(K)e^{irK\cos(\theta-\varphi)}dZ_\theta(\omega). \tag{7.69}$$

It is also a coefficient of T_K:

Proposition 4.2.2

$$\Phi(x,y;\omega) = \langle C_n(K)T_K(0;x,y)\frac{dZ}{d\theta}(\omega)\rangle, \tag{7.70}$$

Remark, by using the Fourier expansion of a Brownian bridge Z, this gives

$$\Phi(x,y;\omega) = \frac{iC(K)}{2\pi}\int_0^{2\pi} d\theta e^{irK\cos(\theta-\varphi)}\sum_{n\in\mathbb{Z}^\times}\frac{\zeta_n(\omega)}{\sqrt{2\pi}}e^{in\theta}, \tag{7.71}$$

and by commuting the sum and the integral, which is justified in $L^2(\Omega)$ for each $(x,y) = r\exp(i\varphi)$, we get

$$\Phi(x,y;\omega) = C'(K)\sum_{n\in\mathbb{Z}^\times}\zeta_n(\omega)\int_0^{2\pi} d\theta e^{irK\cos(\theta-\varphi)+in\theta}. \tag{7.72}$$

By taking the new integration variable $\theta - \varphi$, and using the definition of Bessel functions of integer indexes we find

$$\Phi(x,y;\omega) = C"(K)\sum_{n\in\mathbb{Z}^\times}\zeta_n(\omega)e^{in\varphi}J_n(rK). \tag{7.73}$$

Note that $J_{-n}(z) = \overline{J_n(-z)}$.

We must remark that monochromaticity appeared independently from the uncertainty principle. However irreducibility of the representation of isometries is a natural hypothesis from the invariance point of view: it gives more coherence to the visual area (as do characters for simple cells), and it gives a precisely defined *scale* of translational invariance ([154]). Also, it is remarkable that uncertainty minimization is compatible with irreducibility; that is simply because the principle of uncertainty can be enunciated abstractly, in every unitary representation of the Euclidean group.

7.4.3 Gluing, Two Eyes and Two Hemispheres

(From unpublished works that grew around the thesis of Luc Foubert, September 27 in 2007; see [68]. These works reflect discussions with Jacques Droulez, Luc Foubert, Nathalie Rochefort and Chantal Milleret; thanks to ACI NIC 2003-2007.)

The Mathematics we shall use rely on differential topology, probability and stochastic processes. Here, the invariance that comes into play is topological.

A necessary condition for successful action of an animal in the world is the coherence of the information flow in its brain that controls end effectors. We claim that geometrical co-variance facilitates this coherence (cf. Pellionisz and Llinas ([166], [167]). In fact the information flow follows disconnected routes from the sensory end organs to the internal loops and the end effectors, and co-variance helps to accord these routes. The example below concerns coherence between the left and right hemispheres, for treating visual information coming from the four hemi-retina. Cf. Bullier in *TVN* [44], [160], Olavarria in [165], [69].

In general visual systems divide the image-time in several pieces, and reconstruct a global invariance from there; wonderful examples are offered by the facet eye of the common fly, or by the eight eyes of its enemy the spider (cf. [120]). In mammals the two eyes see different but overlapping parts of the world, and in most of them each retina is divided vertically in two overlapping parts sending the left and right world to the right and left hemisphere respectively. Then the visual areas have to combine these four pieces of information for a unified perception. The bundle of neurons that join the right and left primary visual areas is the *corpus callosum*. Its activity must be conjugated with ocular dominance to exploit the four pieces of information in an optimal way.

Most primary sensory areas respect the right-left symmetry, i.e. the two corresponding hemispheres are covariant for right-left symmetry. Note this is not necessarily true for higher visual areas, for instance in birds or humans, at the end of the visual system, the para-hippocampal region is known to have different functions in the left and right hemispheres.

The invariance structures in visual areas depend on the gluing of information between the left and right eyes and the left and right hemispheres. For instance translations of the image from right to left (or the converse) cannot be analyzed in a co-variant way without correct prolongation across the central vertical meridian. Remark that the neurons of each subarea analyze all components in the image-time: position, duration, time and space frequency, energy flow, colors; therefore all these elements are *a priori* concerned by the re-combination. However the gluing can fail sometimes, as we will see on the example of the tupaia (cf. 4.4), because it can appear conflicts between different kind of invariance; these conflicts depend on the manner invariance is implemented. The example we will develop in subsection 4.4 is ON-OFF symmetry and orientation geometry, as in 4.2, in the case of tupaia. In the following discussion we will consider the role of horizontal connections for the construction of invariance, and the adaptation subtending invariance will depend on development, and on rapid adult adaptation.

We now introduce a general abstract model that we name *random gluing*, which aims at explaining how several brain areas can combine divergent information to preserve invariance structures. In this model we take as a guide the definition of manifolds by charts and gluing, the charts being identifications of pieces with certain models, and gluing being smooth maps between these models (cf. for instance [211] for the concept of charts and manifolds), but in our case the charts represent neuronal functions, that are input-output transformations, and the gluing maps are also stochastic operators supported by neurons. Everything here is described with random variables. The resulting inner model E of the external world will be described by parameters that modulate the neuronal activities.

Precisely, we assume the existence of sets $E_i; i \in I$ and random operators Φ_i which transforms the elements φ_i of E_i in neuronal activities ψ_i of brain areas $X_i; i \in I$. (For random processes and operators kernels see [52].) We also assume the existence of random internal operators Φ_{ji}, supported by sets of neurons X_{ji}, transforming the activity ψ_i in X_i into an activity $\Psi_{ji}(\psi_i)$ in X_j. The neurons in X_{ij} can be inter-area or intra-area, and they can be feed-forward or feed-back or horizontal; examples are commissural axons going from one hemisphere to the other, or back projection from $V1$ to LGN, or inside LGN or pulvinar, or internal to $V1$, from layer IV to III and II to V. Here we mainly consider callosal neurons between hemispheres and binocular neurons in each hemisphere.

The input ϕ_{ji} in X_j (coming from X_i) produces an output ψ_{ji}, which can again be transformed by X_{kj} for $k \in I$ into another input φ_{kji} of the set X_k, and so on.

The *compatibility axioms* for gluing are the following:

1) for each pair (i, j) there exist subsets E_{ij} and E_{ji} in E_i and E_j respectively such that for each input $\varphi_i \in E_{ij}$ there exists a unique input $\varphi_j \in E_{ji}$ denoted by $\varphi_j = \Phi_{ji}(\varphi_i)$ such that $\Phi_i(\varphi_i)$ and $\Psi_{ij}(\Phi_j(\varphi_j))$ have the same probabilistic laws;
2) for each triple (i, j, k) we have $\Phi_{ij} \circ \Phi_{jk} = \Phi_{ik}$ on the subset E_{ikj} in E_{ik} which corresponds to both E_{ij} and E_{jk}.

In particular, for each pair (i, j), we have $\Phi_{ij} \circ \Phi_{ji} = Id$.

These axioms are saying, that *in law* the activities represent a coherent world E made by gluing E_{ij} with E_{ji} for all the pairs E_i, E_j. Thus they are in the same spirit than the hypothesis of invariance in law of the orientation map.

Importantly, the satisfaction of these compatibility axioms require in general an active behavior, for example the convergence of the two eyes in the case of binocularity. In fact the preceding axioms can be understood as a particular case of adaptation, requiring that internal connections Ψ_{ji} are able to reproduce some activations created by direct stimuli. This is a form of simulation (cf. [27]).

From that we can formulate the two principles of random gluing:

(i) the compatibility axioms insure that the random variables corresponding to different roads of information are compatible in law when conditioned by the stimuli;
(ii) given (i), the optimality of the gluing process is obtained by maximizing the joint information.

When the axioms are satisfied each area X_i benefits from several compatible entries φ_i, φ_{ij}, and so on, but the information on a parameter e_i transmitted by the waves ψ_i and ψ_{ij} and so on is *a priori* larger than the information transmitted by each process alone, so that the gluing can augment the information on the common output.

The fundamental property of information that underlies this fact is the possible negativity of the 3 by 3 information of three random variables. A, B, C (for instance $A = \psi_i$, $B = \psi_{ij}$, $C = e_i$):

$$I(A;B;C) = I(A;C) + I(B;C) - I((A,B);C). \tag{7.74}$$

(Cf. [47], and section 6, Appendix 1 below.)

In fact $I(A;B;C) \leq 0$ is interpreted (in Physics and in Information theory) as a positive *synergy* between the two observables A, B over C (cf. [139]). For instance, when A and B are two independent variables, it is easy to see that $I(A;B;C) \leq 0$. This is a refinement of the well known fact that the variance of a mean of independent variables is half of the sum of the variances of the two variables.

This relative independence implies the apparently paradoxical fact, that something presented to the central vertical meridian in the visual sphere is more accurately detected with the two open eyes than with only one. In fact it can be twice better, and not only $\sqrt{2}$ times, i.e. the variance on the position can be divided by four, and not only 2, because, for this central region, we have in the brain (at least) four independent observations of the event: by two eyes and two hemispheres. For optimality of observation, the four pathways have to coincide in law and to be statistically independent when conditioned by the stimulus.

With respect to the general model, the set I of indexes i has four elements $(R,R), (R,L), (L,R), (L,L)$, the first letter for the eye, right or left, the second for the hemisphere, right or left, cf. figure (7.5). They can be considered as the vertexes of a tetrahedron. The internal processes Φ_{ji} between two eyes come from vertical connections inside the cortex, and between the two hemispheres they come from the callosal connections, joining a zone of one hemisphere to a corresponding zone of the contralateral hemisphere. Note that the central vertical meridian is not represented in the cortex exactly at the boundary of $V1$ and $V2$, but there is a *transition zone*, named TZ, extending the representation over the meridian in the ipsilateral visual field. Let us name $V1$-proper the complement of TZ in $V1$, then there exist neurons sending their axons through the corpus callosum from $V1$-proper to TZ (contralateral to ipsilateral) and other sending their axons from TZ to $V1$-proper (ipsilateral to contralateral). See [160], [165].

The uni-ocular hypothesis of Olavarria says that the guiding callosal projections connects regions that mainly prefer the same eye. If this is true we see four dominant gluing processes: two interhemispheric between (R,R) and (R,L), or between (L,L) and (L,R), and two intra-hemispheric between (R,R) and (L,R), or between (L,L) and (L,R). Moreover in majority, callosal projecting neurons are not direct projections of callosal neurons. This arrangement permit to satisfy the first compatibility axiom for the edges $((R,R),(R,L))$, $((L,L),(L,R))$, $((R,L),(L,L))$ and $((R,R),(L,R))$ in the tetrahedron. (They form a so called Petrie polygon in the

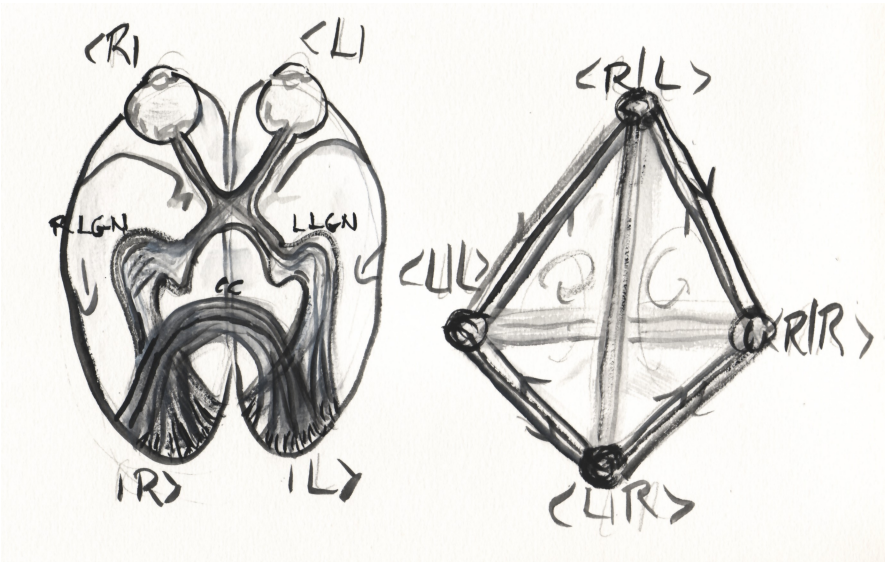


Fig. 7.5 Gluing. Left: the visual pathway form retinae to V1 through LGN, with interhemispheric connections through the corpus callosum. Remark the division of the optical nerve. Right: the symbolic tetrahedron for gluing two eyes and two hemispheres.

tetrahedron.) As those edges form a closed loop, there is one higher relation with four terms to satisfy:

Proposition 4.3.1: A necessary and sufficient condition for the coherent gluing along all edges, faces and volume of the tetrahedron made by two eyes and two hemispheres is

$$((R,L),(R,R),(L,R)) \sim ((R,L),(L,L),(L,R)) \tag{7.75}$$

In fact, as soon as this relation holds, all the others follow: between (R,R) and (L,L) or between (R,L) and (L,R), we conform to one of the two adjacent faces. This way of satisfying all the constraints by satisfying only one is optimal.

Remark that (7.75) relies on an agreement between the two ipsilateral pathways (R,R) and (L,L) that develop later than contralateral pathways (R,L) and (L,R), so a natural conjecture on the development of ipsilateral connections is that it is constrained by this relation and callosal activity. It is a kind of learning, probably supervised. This hypothesis is in accord with the role of the corpus callosum in the installation of binocularity (cf. [62]).

Another application of the gluing process is the relation between *stereoscopy* and *disparity*. Cf. the four articles written by Freeman, Parker, Schor and Blake in TVN.

Disparity measures the difference between the field kernels of the left eye and the right eye. (The callosal connections contribute to disparity too, but we will neglect

this effect now.) Note that the binocular fusion of information cannot be a static absolute gluing: The eye muscles adapt perception to a certain depth, by *convergence*; this makes the phase and orientation of the stimulus change (more than the modulus of frequency). Consequently it is not completely meaningful to speak of an absolute disparity: depending on the position of the eyes in their orbits the parameters change.

The rotation between the two eyes gives two projections of a $3D$ object on two planes, which *theoretically* can be used to re-construct the $3D$ object. This will give a $3D$ kernel:

$$G(x-x_a, y-y_a, z-z_a, t)e^{i(x\xi+y\eta+z\zeta+t\omega+\varphi)} \tag{7.76}$$

As a product of Gaussian densities is a Gaussian density and the product of exponential is the exponential of the sum, the simplest attempt for an interaction of kernels is provided by multiplication before rectification of separate receptive fields. Note this multiplication concerns the spatial part, not necessarily the time part. We define the projections

$$X_R - X_R^a = A_R(x-x_a) + B_R(y-y_a) + C_R(z-z_a), \tag{7.77}$$
$$Y_R - Y_R^a = D_R(x-x_a) + E_R(y-y_a) + F_R(z-z_a), \tag{7.78}$$
$$t_R = t - t_a^R, \tag{7.79}$$
$$X_L - X_L^a = A_L(x-x_a) + B_L(y-y_a) + C_L(z-z_a)), \tag{7.80}$$
$$Y_L - Y_L^a = D_L(x-x_a) + E_L(y-y_a) + F_L(z-z_a), \tag{7.81}$$
$$t_L = t - t_a^L. \tag{7.82}$$

Then for the binocular cell we define

$$G(x-x_a, y-y_a, z-z_a, t) = \\ = G(X_R - X_R^a, Y_R - Y_R^a, t_R)G(X_L - X_L^a, Y_L - Y_L^a, t_L). \tag{7.83}$$

And we get the following assertion:

Proposition 4.3.2: If the receptive field of a binocular cell is obtained by multiplication of two independent uni-ocular linear receptive fields, then the preferred $3D$ frequency vector is given as a function of the Euler angles between the two eyes by the following linear formulas:

$$\xi = A_R\xi_R + A_L\xi_L + D_R\eta_R + D_L\eta_L, \tag{7.84}$$
$$\eta = B_R\xi_R + B_L\xi_L + E_R\eta_R + E_L\eta_L, \tag{7.85}$$
$$\zeta = C_R\xi_R + C_L\xi_L + F_R\eta_R + F_L\eta_L. \tag{7.86}$$

In these formulas, we have four fixed frequencies, expressing disparity when the eyes are parallel, and twelve parameters coming from six independent parameters of rotations of the two eyes. Remark that multiplication of the complex waves added the phases of the uni-ocular RFs; a more reasonable model would be provided

by multiplication of the real parts, giving two components of frequency, one for addition of the phases and the other one for substraction. Also, observe that this simple multiplication of linear kernels would give $\omega = \omega_R + \omega_L$, which is difficult to justify.

More elaborate models, based on the same idea of non-linear composition of two linear fields were studied by Ohzawa, DeAngelis and Freeman; see [157], [158].

Experiments have put in evidence cortical maps for disparity (ex. in area 18), it would be nice if, in cats or macaques, they subtend a grouping by similar $3D$ orientation, or at least an invariance under $3D$ displacements.

Remark: many examples of subcortical gluing exist for the visual system. For instance ([58]) in frogs each retina sends axons to the contralateral tectum only, and there is no direct connection between the two parts of the tectum, but the nucleus isthmi (IN) connects both tectal lobes (T). It receives from ipsilateral tectal lobe and projects bilaterally. Remark: this is not the case in most species, where projection from IN to T is ipsilateral only, for example most fishes (exception for electric fish) and reptiles (exception turtle) and birds. In birds binocular information is already present in the thalamus. There is an homolog in mammals: a bilateral projection to the superior colliculus SC from the parabigeminal nucleus ([78] for cats, [15] for monkeys).

7.4.4 The Strange Gluing of the Tupaia

(This model was discussed during the ACI NIM (2005-2009) and profited in particular of discussions with Chantal Milleret and Nathalie Rochefort.)

The question was: why do the callosal connections of the Tupaia disregard orientation preference?

Tupaia, or three shrew, is a strange animal, which was considered a long time the direct ancestor of primate (cf. [63]). Although it has laterally situated eyes, by turning the retina inside the orbits it has developed a fine frontal vision, with a large binocular domain, apparently useful to detect and select its smaller prays. Thus we have here a strong example of adaptation, enforced by anatomy. The tupaia has precise callosal connections respecting retinotopy. Its area $V1$, including TZ (transition zones) has superb orientation maps, which are respected by numerous intra-hemispheric horizontal connections.

However amazingly Bosking et al. [32] have shown that the callosal connections of the tupaia do not set up any correspondence between the orientation maps in the two hemispheres.

To the contrary the cat has no problem setting up this correspondence (Rochefort et al. [186]).

We will show now that this apparent neglect of invariance results from the insistence of the tupaia to maintain a separation between the ON and OFF pathways in the cortex. This can be seen as the preservation of another structure of invariance, the symmetry between ON and OFF, which is a discrete structure, and which was abandoned in the cortex by other animals, like cats and monkeys. We will show that this ON/OFF structure blocks the callosal gluing of the action of translations and rotations on the representation of orientation, which is a continuous invariance structure on internal parameters.

Because the discussion is somewhat involved we give a summary of the argumentation: (1) In the tupaia the ON/OFF division implies a contralateral ocular dominance in the layers II/III; (2) the orientation preference and its selectivity rely on parallel arrangements of axons of ON and OFF cells and horizontal connections; from (1) and (2) it results that (3) at the time callosal connections are selected the orientation preference is already stabilized in $V1$ proper and in TZ, thus (4) it is too difficult for a callosal connection to respect both position and orientation.

Remarks: (1) means that the discrete symmetry between ON/OFF enters in conflict with the binocular symmetry in adult animals; (2) relies on the connectivity underlying the emergence of the internal representation of orientations; (3) underlines the role of time in development; (4) underlines possible competitions between two continuous representations, here retinotopy and orientation. We saw in section (on pi), that orientation maps has an invariance in law under planar displacements, here we see the difficulty to extend this invariance for both hemispheres and both ocular dominations. This shows that evolution had to fight for invariance.

(1) The organization of the visual systems of mammalian species lies on common principles, but it also shows a number of variations. Cf. Casagrande and Xu in TVN. One of the common principles is the division ON/OFF of the visual information flow. Certain bipolar cells in the retina specialize to be center-ON (excited by light in the center of the RF), others specialize to be center-OFF (excited when light is absent in the center of the RF) (cf. Nelson and Kolb in TVN), then two information pathways take birth: the ganglion cells, sending axons out of the retina, are principally of three types: ON-cells, excited when the intensity of light augments in the center (of RF), OFF-cells excited when the intensity of light diminishes in the center, and ON-OFF-cells excited when light augments or diminishes in the center. The first two sorts emit spikes as long as the intensity does'nt change, but the third one emits spikes only when intensity varies in time. Another division superposes to the ON/OFF division: ganglion cells can be tonic (permanent spiking) or phasic (transient spiking); in carnivores (as cat, dog, ferret or mink) this corresponds to X and Y cells respectively. There exists a third class, named W of smaller and slower neurons. Note the homology with primates is difficult to precise, because X and Y are large and quick as are the magnocellular M cells, and W cells correspond to parvocellular P cells, however P and M neurons of primates have physiological properties which correspond to the characters of X and Y respectively, and the K cells (koniocellular) of primates are similar to W cells.

On the road between retina and cortex, in the dorsal lateral geniculate nucleus of the thalamus (dLGN) of most species of mammals, there exist layers (less precise in small rodents but already visible in rats; they are six in the carnivores and two in the rats), which continue to segregate ON, OFF or ON-OFF, and phasic or tonic. However these layers are disposed differently according to the species. For instance the LGN of cat has six layers A, A1, CM, C1, C2, C3 (plus a MIN and a Wing), cf. [165] ch.I, and Sherman and Guillery in *TVN*; the three first ones are dorsally situated containing X and Y cells, the three others (collectively named CP) are more ventrally situated and containing W cells. The layer A receives both X and Y from the contralateral eye, it has a gradient from X outside-dorsal to Y inside-ventral, A1 is homolog to A for the ipsilateral eye, CM is contralateral but receives only Y, the CPs are all of type W: C1 ipsilateral, C2 contralateral and C3 binocular. From the ON/OFF point of view (cf. [35]), there is in A and A1 a gradient in the Y-region from Y-ON outside-dorsal to Y-OFF inside-ventral, and CM is dominated by OFF. However most specialists consider that the division ON, OFF in the LGN of cats is subtle. In ferret or mink the division is more pronounced, there exist two sub-layers in A and in A1, a dorsal dedicated to ON and a ventral dedicated to OFF. In macaques (as in known old world monkeys and probably in humans, but not in new world monkeys) from dorsal to ventral the layers are denoted from 6 to 1; observations in macaques show that the layer 6 is contralateral and ON, the 5 is ipsilateral and ON, the 4 is contralateral and OFF, the 3 is ipsilateral and OFF, the 2 is is ipsilateral and mixed ON-OFF, the 1 is is contralateral and mixed ON-OFF ([144]). The layers 1 and 2 receive M and K ganglion cells and project to superficial regions of layer IV in V1.

In cats and monkeys, when the information flow arrives in the cortex, it is difficult to observe a separation between ON and OFF; in ferrets it is possible to discern patches which are OFF (cf. [249]). But the tree shrew decided to maintain a strict division between ON and OFF in LGN and to maintain this division in the cortex. In this animal species the layers are organized as in primates from 6 to 1, but only the 6 (which is contralateral) presents a mixture ON-OFF, the 5 is ipsilateral and OFF, the 4 is contralateral and OFF, the 3 is ipsilateral and ON, the 2 is is contralateral and ON, the 1 is is ipsilateral and ON. Thus 4 behaves as in primates but 3, 2, 1 behave at the opposite. The layer 5 is OFF in tree shrew but ON in monkey; the mixing in 6 replaces the mixing in 2 and 1.

The primary visual cortex of the tupai is divided in many layers and sub-layers (cf. Fitzpatrick [66]); the most external sub-layer in the layer IV, which is named IVa, receives LGN axons from 1 and 2 which are exclusively center-ON (remark in the macaque the homologous sub-layer receives also from 1 and 2 but these layers are mixed ON-OFF), the sub-layer IVb receives from 4 and 5 which are exclusively OFF (in the macaque the homologous sub-layer receives also from 4 and 5 but 4 is OFF and 5 is ON thus the ON/OFF information is mixed). Consequently the tupai is ON in IVa and OFF in IVb. Moreover the up of IVa and the bottom of IVb are binocular, but the middle (bottom of IVa and up of IVb) is uni-ocular, exclusively contralateral; this is due to the fact that 2 and 4 are contralateral (which is not the

case in macaque, where 4 is contra and 2 is ipsi). And it is only at this frontier between IVa and IVb that ON and OFF are mixing in tupai's V1. Cf. figure (7.6).

(2) The origin of columns of orientation preference, even if not fully understood, takes advantage on alignments of center-ON projections and center-OFF projections, as it was suggested initially by Hubel and Wiesel. Mooser, Bosking and Fitzpatrick have proved in 2004 ([146]) that orientation preferences in $V1$ of the tupai are established inside the cortex, not at the arrival from LGN. This result is compatible with the separation of ON and OFF until there. In tupai, the alignments of ON and OFF are formed by horizontal connections in $V1$; they can exist only higher than IVa, in sub-layers IIIb and higher, where the neurons of IVa (which are ON) and IVb (which are OFF) project. Note that certain neurons in IV of the tupai are selective for orientation, but the layer IV doesn't contain long horizontal connection. Moreover orientation selectivity is stronger in layers II/III than in IV (cf. [66]). The long distance connections joining similar orientation columns are mostly present in II/IIIa,b (Bosking, Fitzpatrick et al. [33]et al. and before them Rockland and Lund, [187]). Note these results confirmed the important role of horizontal connections for orientation selectivity. (Remark in the tupai the patches of axonal terminations are preferentially aligned with the preferred orientation ([76]), which is not sure in the cat or the macaque ([134]).)

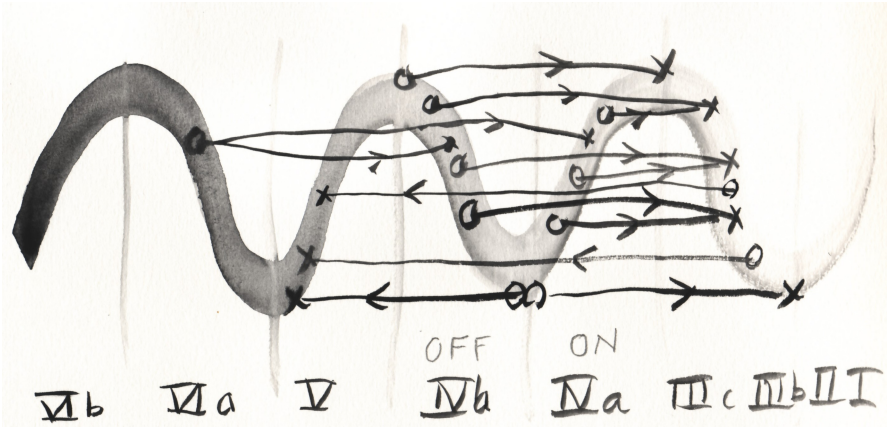


Fig. 7.6 Folding. The six layers of V1 of tupaia, with its vertical projection, according to Fitzpatrick [66]. Remark the functional folds, invariant by the connections.

To summarize what we wrote until now, the choices made by the evolution for the tree shrew have implied two consequences: (1) in the layers II/III the cortex is strongly dominated (if not exclusively) by the contralateral eye; (2) the orientation

selectivity is mostly present in these layers II/III (or in the symmetric layers V/VI), which are also the layers where intra-hemispheric connections exist.

(3) The corpus callosum has its own developmental rules. Kretz and Rager ([117]) have studied this development in the tupai; they found that, from P7 to P9 few callosal connections appear in layer III but more appear in layer VI (where there is minor orientation selectivity at that time), from P10 to P13 supra-granular connections grow, their extension attains a maximum around P13, then between P13 and P15, 95% of these connections disappear! After this date the configuration is almost the same as the one in adult animals. Most of the connections now are belonging to III, they have disappeared from VI after P15, but the installation was driven by the connections in layer VI. Note that in the infra-granular layer VI the information on the place in visual plane and the orientation selectivity are installed between P7 and P17. At the end most callosal connections rely $V1$ (or 17) with the transition zone TZ (or 17/18), but there is also in tupai, contrarily to what happens in the cat and monkey, many heterotopic connections from TZ to 17 or 18, covering all the binocular field. Thus retinotopical gluing is also a little perturbed in tupaia.

In cats the construction period of callosal connections is much longer (cf. [145], [5]), but the principle is the same: elimination of exuberant connections which appear during the first days after birth (see [93]). In the first days after birth, callosal connections (or better varicosities) appear in all layers I,...,VI ([62]); then during two months these connections regress and subsist only between TZ and $V1$ or reciprocally. The same happens for the rat. In the case of ferret, inside the binocular region, which is exceptionally large (20 degrees in the contralateral field), most neurons are binocular but the ocular dominance has a patchy structure. The callosal connections are also patchy ([187]). There are more infra-granular callosal connections in ferrets than in cats ([36]). In old world monkeys (as us) callosal connections are formed before birth ([108]). Note this is an elegant way to solve the gluing problem: make connections before you choose preferences for position and orientation, and use these connections for coherence of preferences. Monkeys do that by establishing callosal connections before birth, and cats by forming the ipsilateral map by copying the contralateral one through callosal connections with TZ.

(4) Thus, in $V1$ of the tupaia the inter-hemispheric connections connect cells already dedicated to a well defined place, respecting visuotopy (cf. Olavarria [160]), however all these cells at that time have already chosen their preferred orientation, thus the callosal connections have few chance to respect orientation if it respect position.

The fact that orientation preference was prematurely determined is due to the dominance of the area by the contralateral eye, which results from the logic of the ON/OFF repartition.

So the impossibility of adaptation of connection for respecting orientation implies a defect of invariance.

(5) Supplementary discussion: we examine now the link between what precedes and the hypothesis that callosal connections are mainly driven by information coming

from one eye. This driving is the uni-ocular hypothesis of Olavarria that we discussed in section 4.3.

At first sight this hypothesis seems to contradict the well established fact that horizontal connections respecting the orientation preference exist between neurons which different ocular dominance as frequently as between neurons with the same ocular dominance (cf. [165]). However, in all species we are considering, the orientation maps have began to form before the eyes are opening almost without visual experience (cf. [233]), thus orientation maps begin to form in a cortex which is dominated by the contralateral eye. Then the orientation map for the columns that are dominated by the ipsilateral eye have to follow the contralateral map, extending it by continuity, with a relative freedom for variability. Note this second map can become dominant after occlusion of the contralateral eye.

A convincing explanation for the reinforcement of a synapse is the idea of Hebb, that the synapse becomes stronger when the postsynaptic neuron is excited after the presynaptic one was excited. According to Löwel and Singer, [132], cats which undergone a unilateral resection of the medial rectus muscle between age P15 and P21, are developing long range connections between domains which are controlled by the same eye, and according to Schmidt et al. [198], in cats with strabismus, the selectivity to orientation is not modified but the long range connections connect domains with similar orientation preference.

The biochemical and genetical processes, involving cadherins, NMDA-NRs, CREB, PKA,..., which are responsible of the stabilization of intra-cortical synapses, are changing their expression with developmental time; the fact that horizontal connections between opposite eyes arrive later than the ones between the same eye could be a sufficient reason for a different chemical expression, not relying on coincidence.

Before eye opening there exists a cortical activity which is modulated by visual stimuli and by natural motions ([6]). Spontaneous activity happens in the retina, in LGN and in the cortex (cf. [165]). For instance, in the LGN, it exist inter-hemispheric correlations of activities (cf. [231]), however most of these correlations should imply uni-ocular correlations and the pathway with same preference ON or OFF. Importantly there exists a difference of activity that distinguishes between contralateral and ipsilateral domination: there is more correlation for neurons informed by the same eye, and even more in the case of contralateral eye, and they can group ON or OFF separately or ON and OFF together; this activity can contribute to the formation of orientation columns. After eye opening exchanges of information exist between neurons of different ocular dominance: an ipsilateral map extends the contralateral map, and hetero-ocular connections happen.

According to Weliky and Katz [230], studying the development of the ferret, the horizontal connections begin to form at the moment where eyes are opening, at a time where the contralateral eye dominates. After eyes opening the orientation maps development becomes dependent on visual experience (NMDA regulation and CREB expression).

In tupaias, the layers II/III in V1 are monocular, thus intra-hemispheric horizontal connections are necessarily contralateral-contralateral, and inter-hemispheric con-

nections are necessarily contralateral-ipsilateral, consequently they cannot be homo-ocular and going from II/II to II/III. Casagrande and Condo ([43]) have shown that, after unilateral enucleation at birth, the LGN layers of the tupaia controlled by the resting eye are preserved, but in the cat they are not; this indicates that the visual system of the tupaia is more uni-ocularly driven than the visual system of the cat. In cats and monkeys interaction between eye's domination appears important for normal development.

7.5 Higher Levels of Invariance

7.5.1 General Covariance in $V1$

(Prepared during ACI NIM 2005-2009, profited of many discussions with Jean Petitot and Pierre Baudot, and in other contexts with Jean-Pierre Nadal and Alessandro Sarti.)

Our main hypothesis about $V1$ is the presence of a *continuous invariance*, compatible with topological invariance. This invariance, at the opposite of a global invariance (as it happens for example in the fusiform gyrus for faces), has a local character: it postulates that stimuli which can be deduced one from each other by smooth deformations generate equivalent activities of different assemblies. For instance, it is known that a static line of dots L with convenient orientations generate a rebound activity $s \mapsto A(s,L)$ of the neurons in $V1$; cf. [111]. And there is no evidence that in $V1$ straight lines give more activation than curved lines, with not too large curvature. Then our hypothesis is that, if φ is a sufficiently small and sufficiently smooth homeomorphism of the visual plane, in particular not disturbing too much the curvature, there exists a bijective remapping $T(\varphi)$ of the $V1$ subunits such that the activity $s \mapsto A(s,\varphi(L))$ in $V1$ which is generated by the presentation of the line $\varphi(L)$, is (almost) equal to the activity $s \mapsto A(T(\varphi)^{-1}(s),L)$. The term "almost" here can be understood in a probabilistic sense, in accord with models by random processes.

The movement of a dots line L_t (where t denotes the time coordinate) generates an activity in time A_t, which cannot in general be deduced by just adding the above functions $A(L_t)$ (cf. [107]); our hypothesis in this case is the existence for any family of small deformations φ_t in the visual plane, of a family of bijections T_t such that for almost all s we get $A_t(T_t(s),\varphi_t(L_t)) = A_t(s,L_t)$. Another example is given by a sequence in time, i.e. the dots are not presented all together but one after each other in a certain order (cf. [129]). Here it is more convenient to speak of co-variance than invariance.

In $V1$ we find an approximate symplectic co-variance; it correspond to the symplectic group in dimension $2(2D+1)$ acting on the co-tangent space of the product of the visual plane by the time axis, and it is extended to $2(3D+1)$ if we take in account disparity. The parameters that are concerned are position and frequencies, spatial and temporal; they form a vector in a space of dimension 8. These parameters are almost uniformly distributed; in fact there are two populations, one for

for high spatial frequency and low temporal frequency, another one for the opposite. But this symplectic repartition of receptive fields is not sufficient to explain the diffeomorphism invariance; we need for that an organization of ensembles, for instance a convenient map of preferences, and horizontal connections, lateral exchanges, non-linear excitation-inhibition, loops with the Thalamus and feed-back return from the cortex. See Bullier and Van Essen in TVN. For instance $V2$ activity commands illusory lines that can appear in $V1$. Cf. [123]. Remark that an orientation maps seems to be unnecessary for high discrimination, as shows the example of the squirrel (cf. [219]).

Schematically, one can say that $V1$ (and probably $V2$) has a continuous horizon for its functional invariance, and is aimed to construct a sort of differential topology and differential geometry by itself, taking in account information of other areas. This doesn't exclude elaborate individual responses of neurons in $V1$, whom receptive field take in account complex characteristics of natural images. Cf. P.Baudot results ([19]). To the contrary, a high dimensional covariance allows the computation of higher correlations (or higher mutual information) in images, for recognition of complex forms. From its differential topology and differential geometry the area $V1$ contributes to the recognition of discrete invariants.

The areas $V1, V2$ can be seen as vectors of operators acting on image-movements (and transforming it into spikes fields), thus the more adapted pseudo-group for them is not the pseudo-group of diffeomorphisms but its extension, the pseudo-group of symplectomorphisms , acting on the cotangent space over space-time, by respecting the natural symplectic structure (cf. [207], [228]). This is also the natural symmetry of light rays bundles. As we suggested in 3.1 pseudo-differential operators represent function of assemblies in $V1, V2$, and the natural (pseudo)-group of symmetry for them is made by symplectomorphisms ([228]). In certain problems a more natural choice could be the Contact transformations, i.e. homogeneous symplectomorphisms; in this case the role of space is played by contact elements, i.e. pairs of a point and a co-direction.

This general covariance in $V1$ could also be extended to color information, a good candidate for that being a pseudo-group of Gauge transformations over the symplectomorphisms pseudo-group. Note this pseudo-group can be seen as a pseudo-group of transformations that respect a Poisson structure. Cf. [229].

7.5.2 Projective Invariance in $MT+$

The invariance in areas MT, MST, which are interested by movements in the image, is probably of high dimension, as in $V1, V2$; however in these areas it appears also a finite dimensional invariance given by projective deformations that we want to describe. It would be interesting to look at the possibility of a localization of this projective geometry in MT or MST.

A simple model of linear summation of non-linear activities of $V1$, followed by a static non-linearity is sufficient to explain how receptive fields in MT of primates detect the speed of objects with respect to the retina (see [193]).

Neurons in the MT complex (MT, MST) integrate the *optic flow*.

Our presentation of the optic flow is inspired by Koenderink and VanDoorn [112], [115] and Ken-Ichi Kanatani (IEEE 1988) [103].

We consider the Euclidean space $E = \mathbb{R}^3$, I_3 denotes the canonical frame, and G the group of displacements (direct isometries).

The movement of an orthonormal frame is described by a smooth map $R : I \to G$, where I is an open interval in $\mathbb{R}$. We note O_t the center of the moving frame, and $\rho(t)$ in SO_3 the linear part of $R(t)$. It is easy to show that the derivative of R in $t_0 \in I$ can be written

$$DR(t_0).s = sV(t_0) + sA(t_0)\rho(t_0), \tag{7.87}$$

where $V(t_0)$ is a $3D$ vector, named the linear derivative of R en t_0 and where $A(t_0)$ is a 3×3 antisymmetric matrix, named the angular speed of R in t_0.

We introduce the $3D$ vector Ω whose components in the fixed frame I_3 are $\Omega_1 = -a_{23}, \Omega_2 = +a_{13}, \Omega_3 = -a_{12}$; then for every $X \in \mathbb{R}^3$ we have:

$$A.X = \Omega \times X, \tag{7.88}$$

where the crux denotes the usual vector product.

This vector Ω is named the angular speed vector (viewed in the fixed frame).

An orthonormal base change P that transforms A into $A' = PA^tP = PAP^{-1}$ changes Ω into $\Omega' = P\Omega$.

Let Q be a fixed point in E; denote by $q(t)$ the trajectory of Q in the moving frame R; we get

$$\frac{dq}{dt}(t) = -v(t) - \omega(t) \times q(t); \tag{7.89}$$

where $R(t)v(t) = V(t)$ and $\rho(t)\omega(t) = \Omega(t)$.

Proof: we have $q(t) = R(t)^{-1}Q$, thus

$$\frac{dq}{dt}(t_0) = -R(t)^{-1}DR(t)q(t) \tag{7.90}$$

$$= -R^{-1}(V + A\rho q) \tag{7.91}$$

$$= -R^{-1}V - \rho^{-1}A\rho. \tag{7.92}$$

We finish by using the correspondence between A and Ω.

When Q is moving in I_3, its trajectory $Q(t)$ has a speed $\dot{Q}(t)$; we obtain

$$\frac{\partial Q}{dt}(t) = -V(t) + \dot{Q}(t) - \Omega(t) \times Q(t). \tag{7.93}$$

This gives in the moving frame

$$\frac{dq}{dt}(t) = -v(t) + R^{-1}(t)\dot{Q}(t) - \omega(t) \times q(t). \tag{7.94}$$

We will write $v_q = v - R^{-1}\dot{Q}$.

We assume $Q \neq O_t = R(t)(O)$, then we define the *proximity* $\mu = 1/\|q\|$, and the *visual point* $\sigma = \mu q$. The norm of this vector is equal to 1, we consider it as a moving point in the unit sphere Σ of R_t, it represents how appears Q for a cyclopean observer in O_t with eye moving like $\rho(t)$ with respect to the fixed reference frame I_3.

Proposition 5.2.1: in the moving frame we have

$$\frac{d\sigma}{dt}(t) = \mu(t)(v_q(t) \times \sigma(t)) \times \sigma(t) - \omega(t) \times \sigma(t). \tag{7.95}$$

Proof: the derivative of $\|q\|$ is $\mu q.\dot{q}$; then the derivative of μ is $-\mu^3 q.\dot{q}$, consequently

$$\frac{d\sigma}{dt} = -\mu^3(q.\dot{q})q + \mu\dot{q} \tag{7.96}$$

$$= \mu((-\sigma.\dot{q})\sigma + (\sigma.\sigma)\dot{q}). \tag{7.97}$$

However, for any triple of vectors (a,b,c) we have

$$(a \times b) \times c = (a.c)b - (b.c)a. \tag{7.98}$$

Thus

$$\frac{d\sigma}{dt} = \mu(\sigma \times \dot{q}) \times \sigma \tag{7.99}$$

$$= \mu((v_q + \omega \times q) \times \sigma) \times \sigma \tag{7.100}$$

$$= \mu(v_q \times \sigma) \times \sigma + ((\omega \times \sigma) \times \sigma) \times \sigma \tag{7.101}$$

$$= \mu(v_q \times \sigma) \times \sigma - \omega \times \sigma. \tag{7.102}$$

Observe that $v_q \times \sigma) \times \sigma$ is the projection of v_q on the tangent plane of Σ.

By considering a point Q in each direction σ of Σ the formula of prop.1 gives a vector field Φ, depending on time, tangent to the sphere Σ:

$$\Phi(\sigma) = \mu(\sigma)(v(\sigma) \times \sigma) \times \sigma) - \omega \times \sigma. \tag{7.103}$$

It is this vector field which is called the *optic flow*.

In general Φ has discontinuities along the apparent contour of visible surfaces, then it cannot be integrated in transformations of Σ. But we will consider a natural case where where Φ is of class C^1.

Remark that to compute with Φ it is better to project Σ on a plane attached to the moving frame. This corresponds to the usual rules of optics: the gaze is directed along e_3 and the image is interpreted as a projection from O_t on a plane perpendicular to e_3.

Let ρ be the distance from O_t to this plane, and (x,y) the Cartesian coordinates of the image of σ in a frame e_1, e_2 (fixed with respect to $R(t)I_3$). Let us note v_1, v_2, v_3 and $\omega_1, \omega_2, \omega_3$ the coordinates of v and ω respectively. If the coordinates of σ in $R(t)I_3$) are (x_1, x_2, x_3), we have

$$x = \rho \frac{x_1}{x_3}, \quad y = \rho \frac{x_2}{x_3}. \tag{7.104}$$

Then

$$\frac{dx}{dt} = \frac{\rho}{x_3}\frac{dx_1}{dt} - \frac{x}{x_3}\frac{dx_3}{dt}, \quad \frac{dy}{dt} = \frac{\rho}{x_3}\frac{dx_2}{dt} - \frac{y}{x_3}\frac{dx_3}{dt}. \tag{7.105}$$

On another side Φ can be written in the coordinates x_k as follows:

$$\frac{dx_1}{dt} = \mu[(v.\sigma)x_1 - v_1] - \omega_2 x_3 + \omega_3 x_2, \tag{7.106}$$

$$\frac{dx_2}{dt} = \mu[(v.\sigma)x_2 - v_2] - \omega_3 x_1 + \omega_1 x_3, \tag{7.107}$$

$$\frac{dx_3}{dt} = \mu[(v.\sigma)x_3 - v_3] - \omega_1 x_2 + \omega_2 x_1. \tag{7.108}$$

Thus

$$\frac{dx}{dt} = \mu[(v.\sigma)x - \rho\frac{v_1}{x_3}] - \rho\omega_2 + \omega_3 y \tag{7.109}$$

$$- x\mu[(v.\sigma) - \frac{v_3}{x_3}] + \frac{1}{\rho}\omega_1 xy - \frac{1}{\rho}\omega_2 x^2 \tag{7.110}$$

$$\frac{dy}{dt} = \mu[(v.\sigma)y - \rho\frac{v_2}{x_3}] + \rho\omega_1 + \omega_3 x \tag{7.111}$$

$$- y\mu[(v.\sigma) - \frac{v_3}{x_3}] + \frac{1}{\rho}\omega_1 y^2 - \frac{1}{\rho}\omega_2 xy. \tag{7.112}$$

or in other terms

$$\frac{dx}{dt} = \mu\frac{xv_3 - \rho v_1}{x_3} - \rho\omega_2 + \omega_3 y + \frac{x}{\rho}(\omega_1 y - \omega_2 x), \tag{7.113}$$

$$\frac{dy}{dt} = \mu\frac{yv_3 - \rho v_2}{x_3} + \rho\omega_1 + \omega_3 x + \frac{y}{\rho}(\omega_1 y - \omega_2 x). \tag{7.114}$$

Here x_3 is given by the formula

$$\frac{1}{x_3} = \sqrt{1 + x^2 + y^2}, \tag{7.115}$$

which says that σ has norm 1.

A first use of the registering of an optic is for estimating the distance of the subject (assimilated to O_t) to objects in the space E. We simplify by considering only N points Q_i.

Theorem 5.2.1: Assume $N \geq 6$, all σ_i distinct, and O_t does'nt displace in the direction of at least 6 of the Q_i; then the optic flow equations allows to determine v, ω and all the μ_i such that O_t does'nt displace in the direction of Q_i.

This an application of the implicit function theorem.

Now we consider the projective invariance hidden in the optic flow. For that purpose we look at points Q that belong to a fixed plane Π of the space E. Then, for each time, fro each point σ in Σ, the proximity $\mu(\sigma)$ is equal to the quotient $\delta(\sigma)/\delta$ of the distance $\delta(\sigma)$ of O_t to the plane $\Pi(\sigma)$ that is parallel to Π containing σ, by the distance δ from O_t to Π. (Just apply the Thalès theorem.)

But $\delta(\sigma)$ is a linear combination of the coordinates x_k:

$$\delta(\sigma) = \alpha x_1 + \beta x_2 + \gamma x_3. \tag{7.116}$$

By combining with the above equation of Φ in the coordinates x, y, this gives

$$\frac{dx}{dt} = \frac{1}{\delta}(xv_3 - \rho v_1)(\alpha x + \beta x + \gamma) - \rho\omega_2 + \omega_3 y + \frac{x}{\rho}(\omega_1 y - \omega_2 x), \tag{7.117}$$

$$\frac{dy}{dt} = \frac{1}{\delta}(yv_3 - \rho v_2)(\alpha x + \beta x + \gamma) + \rho\omega_1 + \omega_3 x + \frac{y}{\rho}(\omega_1 y - \omega_2 x). \tag{7.118}$$

We obtain an element of the eight dimensional family of vector fields that can be written

$$\frac{dx}{dt} = u + Ax + By + x(Ex + Fy) \tag{7.119}$$

$$\frac{dy}{dt} = v + Cx + Dy + y(Ex + Fy). \tag{7.120}$$

This family has a simple geometrical interpretation: the projective group $PGL(E)$ (that is the quotient of the linear group $GL(E)$ by the scalar multiplications) acts on the set $\mathbb{P}(E)$ of straight lines through O_t in E. This set is a (non-orientable) manifold of dimension 2. If we consider the coordinates x_1, x_2, x_3 on E, an open set U_3 of $\mathbb{P}(E)$ is formed by the lines that meet the plane $x_3 = \rho$, where x, y are coordinates. Every matrix in $SL_3(\mathbb{R})$ (of determinant equal to 1) sufficiently near the identity can be written $\exp(X)$ where X has trace zero, i.e. $X \in sl_3(\mathbb{R})$. Let us define

$$X = \begin{pmatrix} a & b & c \\ d & e & f \\ g & h & k \end{pmatrix} \tag{7.121}$$

The fact that $X \in sl_3(\mathbb{R})$ is expressed by $k = -a - e$.

Proposition 5.2.2: The derivative $d(\exp(\varepsilon X))/dt$ in $\varepsilon = 0$ induces in U_3 a vector field of the preceding form.

Proof:

$$\frac{dx}{d\varepsilon}|(\varepsilon = 0) = \frac{\rho}{x_3}\frac{dx_1}{d\varepsilon}(0) - \frac{\rho x_1}{x_3^2}\frac{dx_3}{d\varepsilon}(0) \tag{7.122}$$

$$= \rho(ax + by + c) - \frac{1}{\rho}x(gx + hy + k). \tag{7.123}$$

$$\frac{dy}{d\varepsilon}|(\varepsilon=0) = \frac{\rho}{x_3}\frac{dx_2}{d\varepsilon}(0) - \frac{\rho x_2}{x_3^2}\frac{dx_3}{d\varepsilon}(0) \tag{7.124}$$

$$= \rho(dx+ey+f) - \frac{1}{\rho}y(gx+hy+k). \tag{7.125}$$

Remark: by taking in account the relation $k=-a-e$, and introducing $\nu=\rho+\rho^{-1}$, we get

$$\frac{dx}{d\varepsilon} = \rho c + (\nu a+\rho e)x + \rho by - \frac{x}{\rho}(gx+hy) \tag{7.126}$$

$$\frac{dy}{d\varepsilon} = \rho f + \rho dx + (\rho a+\nu e)y - \frac{y}{\rho}(gx+hy) \tag{7.127}$$

The above proposition tells that the optic flow for a fixed plane is the generator of a projective transformation.

An orthonormal change of frame P transforms $X \in sl_3(\mathbb{R})$ into $PXP^{-1} = PX^tP$; this defines a linear action of SO_3 on sl_3, that is a vector space of dimension 8. This linear representation is the direct sum of two irreducible representations, the first one, of dimension 3, on the antisymmetric matrices, identified to the rotation speed vector ω, the second one, of dimension 5, on the vector space of symmetric matrices with trace zero. We will note them respectively E_3 and E_5, and we will denote by a and B respectively their generic elements.

We also introduce the five following functions: $f(a) = \|a\|^2$, $F(B) = \|B\|^2 = Tr(B^2)$, $G(B) = Tr(B^3)$, $g(a,B) = a.Ba$, $h(a,B) = a.B^2a$. These functions are smooth and invariant under the action of SO_3. We will note $\varphi = (f,F,G,g,h)$ the map from sl_3 to $\mathbb{R}^5$.

Note there is a natural prolongation of the action of SO_3 on $E_3 \oplus E_5$ to the full orthogonal group O_3; this prolongation is the natural action of O_3 on E_3 and the action by conjugation on E_5; only this second one comes from the action by conjugation of O_3 on sl_3. It is easy to show that O_3 acts transitively on each fiber of the map φ from sl_3 to $\mathbb{R}^5$. We deduce that all the fibers of φ are smooth submanifolds of sl_3, because they identify to homogeneous spaces O_3/H. In general this manifold has dimension 3. However there are points in sl_3 where φ is singular (i.e. its derivative is not surjective), for instance when $a=0$ and B has a symmetry of revolution, in this case the orbit is a $2D$ sphere, or when $a=B=0$ where the orbit reduces to a point.

Let W be the set of elements a,B of sl_3 such that a, Ba, B^2a are linearly independent in $\mathbb{R}^3$, and that the principal values $\lambda_1,\lambda_2,\lambda_3$ of B are two by two distinct and non-zero; then W is an open and dense subset of sl_3, invariant under the action of SO_3, and in this open set all points are regular for $\varphi = (f,F,G,g,h)$, thus the application φ from W into $\mathbb{R}^5$ defines a fibration.

Remark that in W there is a discrete invariant for the action of SO_3 in addition of the five functions f,g,h,F,G; this is the orientation of E defined by the frame a, Ba, B^2a. This defines the two connected components of W. The existence of this

discrete invariant implies that the fibers of φ are not orbits under SO_3, and that there exists smooth functions that are invariant under SO_3 that are not functions of f, g, h, F, G. However it is easy to prove from restriction to W the following result:

Theorem 5.2.2: the smooth functions that are invariant under the action of O_3 are the C^∞ function of the five fundamental invariant f, g, h, F, G.

All that connects nicely invariance in vision with classical invariant theory (cf. [232]).

7.5.3 Examples of Geometric Cells

The perception of position in space is organized by the group G of Euclidean displacements. The geometric cells for this geometry are cells that gives an information in a space G/H for a subgroup H of G (see Appendix 1). This sub-group describes the changes in rigid spatial frames that let the cell indifferent.

The examples below are issued from studies in the para-hippocampal system of rats, and rats have developed in their para-hippocampal region a system that is adapted to horizontal displacements thus we will restrict ourselves to the group formed by displacements in the horizontal plane, and we denote by G this group. However primates, in particular humans, possess in the same region cells adapted to displacements in the visual plane (Rolls, [189], and Eckstrom, Fried, cf. [148]), and that bats have a complete $3D$ system ([247]).

The para-hippocampal region stays at the end of the temporal visual pathway. It also belongs to the limbic system, containing the entorhinal cortex (EC), the perirhinal cortex (PRC) and nuclei of Amygdala and Septum. It is a set of areas implicated in sentiment expression.

A very nice reference for this section is [10].

The first invariance that was proved experimentally is *place invariance*: the *place cells* (PCs) were discovered by O'Keeefe and Dostrowski in 1971, in the Hippocampus proper, CA1, CA3 et DG (dentate gyrus). Such cells exist also in the Subiculum, but apparently not in the entorhinal cortex (EC). Here the group H of a cell depends on a place P in the horizontal plane E, it is the subgroup of rotations around P. The quotient $G/H(P)$ identifies canonically with E, but this plane is marked with a point. All the groups $H(P)$ are conjugated in G. The translation from P to P' give a canonical isomorphism from $H(P)$ to $H(P')$.

The second system is the *direction invariance*; here the indifference is the subgroup T of translations. Cells with this invariance are called head direction cells (HDCs), they were found first by Jim Ranck in 1985. Then Taube, Muller and Ranck (1990) conducted a systematic study of HDCs. Such cells exist in the anterior dorsal nucleus of the Thalamus (ADN), the lateral mamillary nucleus (LMN), the medial dorsal entorhinal cortex (dMEC), in the parasbiculum (PaS) and the postsubiculum (PoS), which is part of the presubiculum (PS). A node for the HDC formation is the tegmental dorsal nucleus (DTN). Remarkably this node is at the intersection or three rods of information: a) on proper movement (Habenula), b) on vestibular flow

(medial nucleus), c) on visual information (via PoS). All the HDCs share the same indifference group. The information quotient G/T is the circle of oriented directions of the head in the horizontal plane; it is a group isomorphic to $\mathbb{R}/2\pi\mathbb{Z}$. Then this case is Galoisian: the information itself forms a group. We suggest that this is the reason why direction remapping is coherent, contrarily to the case of place cells: when *HDCs* change their preferences, in general they change by the same angle (there are exception in ambiguous cases where part of the population changes and part does'nt), but when PCs change their preferences, in general there is no relation between the new places of different cells.

Grid invariance is stranger; it was discovered in 2005 in dMEC by Torkel Hafting et al. [80] in the laboratory of M-B.Moser and E.Moser in Trondheim. They are also present in PaS and PoS. In this case the indifference groups of the grid cells (GCs) are discrete subgroups of G, they are the groups H_Γ of direct isometries that fix an equilateral lattice Γ. The group H_Γ is generated by a discrete subgroup of translations T_Γ and by the rotations whose angle are integer multiples of $2\pi/3$ around the vertexes of Γ. The Galois information G/G_Γ is a smooth oriented closed $3D$ manifold that fibers over a two dimensional torus of phases T/T_Γ. Recent data indicate that the directions in T_Γ are the same for all GCs in the same hemisphere; these directions undergo a coherent remapping after change in the environment, for instance rotations of visual cues, but the phases change incoherently like places for PCs.

Frame invariance also exists in the dMEC, PaS and PoS; in this case indifference is reduced to the identity Id of G. The corresponding cells have a preferred place and a preferred direction. There are also cells which prefer a grid and a direction; we could call them *Toric cells* because the information content of the population coincide with a torus T/T_Γ; for this population the life plane is periodic. (See [10].)

Topological invariance is represented by cells coding for coins, boundaries or open sets; they were discovered by Trygve Solstad et al. [206], also in Trondheim with M-B.Moser and E.Moser, in dMEC, PaS, PS. In this case we cannot continue to work with the group of displacements as Galois group, we must start with the group G of diffeomorphisms of the plane, and the indifference groups H are subgroups that fix topological subsets, like coins or boundaries. Note the additional symmetry $ON-OFF$ for cells active on a boundary and cells active in the complementary set of this boundary.

7.5.4 View-Invariant Recognition, Manifolds of Sections

In *TVN* ([44]), many papers are concerned with this topic, for instance R.F. Hess (p. 1043), C.E. Connor (p. 1080), E.T. Rolls (p. 11665), N. Kanwisher (p. 1179), L. Spillman and W.H. Ehrenstein (p.1573), M. Riesenhuber and T. Poggio (p. 1640), W. Singer (p. 1665), C. Koch and F. Crick (p. 1682).

A fundamental property of visual processing and visual perception is the existence of invariant recognition (cf. Bienenstock and Von der Malsburg [29], Wallis, Rolls and Foldiak [226], Lowe [130], Riesenhuber and Poggio [185], Masquelier

and Thorpe [138], ...): different views of an object (or a person or an event), give rise to the perception of this object as a unit (or this person or this event respectively), its identification as a specific entity. A related property is the recognition of similarities between forms or objects. In particular in humans the performances in recognition and detection of similarities are exceptionally good. A lot of researches focused on modeling these invariance properties; the proposed mechanisms were frequently based on temporal association (Foldiak), synchrony (Singer), or polychrony (Tallon-Baudry), ..., cf. the collection edited by Von der Malsburg, Phillips and Singer [224]. A multiplicity of factors are contributing here: compensation, illusions, learning and so on. Most studies insisted on hierarchical processing (a gradual emergence of view-invariant representation, by successive network's computations). Other studies insisted on the structure that prepares invariance in the visual areas, and the variety of forms of invariance beyond (cf. in particular Rolls and Stringer [191], Cadieu, Poggio et al. [41] and Lowe [130]).

In the following paragraphs we try to join our schema of (co-homological) adaptation (2.4) with the remarks we have made on general co-variance in $V1$, for proposing a model of what could be a "stable image" in the brain, and how it could refer to "stable objects". Note we assume that "images" are nothing else than collections of brain cells activities in visual (or multisensory) areas, and that the relations of "images" to "objects" are co-activations with other brain areas, in the sense of temporal association sequences, or at least coherent modulation.

The primary visual areas $V1, V2$ are the reservoir of all images. It is established that even for visual illusions, the primary areas become active. For poor stimuli, the cells in $V1, V2$ behave according to a small number of parameters, but these parameters are non-linearly modulated by horizontal and feedback connections, taking in account larger part of the image. For complex stimuli, as natural images in motion, the cells in $V1, V2$ behave differently, detecting more complex characteristics in the image (cf. [19]). Thus, collectively, the primary activity is adapted to a high dimensional invariance (practically infinite) that we have named general covariance. However, the inner representation of a "stable image of the world around" seems to lack in $V1, V2$. In fact this representation can correspond to the joint activity of higher visual areas, even without units cells for a total view. Note that every image must be the "image of something". We suggest that the "things" in the image correspond to "vanishing cycles", in higher visual areas, in the sense of the internal spaces of 2.4, equivalence classes of attractors combinations. The following paragraphs try to further formalize this suggestion.

1) Let M denotes the manifold of functional parameters of all the cells in $V1, V2$. Remind the parameters of each individual cell form an homogeneous space G/H, for instance the product of the color space with the co-tangent space of a $3D$ model vector space; the color space is homogeneous for the affine group (cf. 3), and the co-tangent spaces made by the frequencies, temporal or spatial and position (retinotopy), is homogeneous for the symplectic group of light rays; then the group G can be taken as the product of these two groups. By retinotopy and disparity (managing stereoscopic depth for binocular cells), the manifold M is fibered over

the $3D$ ambient space E. This allows a mirror in the brain of localization of the images and the objects in the world (cf. [19]). The trace of an image in $V1, V2$ is a mapping from $V1, V2$ to M, i.e. an element of the space of sections $\mathscr{M}$ (cf. 2.4). By general co-variance the spaces of categories $\mathscr{I}$ and the space of contexts $\mathscr{E}$ for $V1, V2$ are infinite dimensional in $V1, V2$. An example of element in $\mathscr{I}$ is a curved contour.

2) Let A be a higher area, for instance $V3, V4, V5, V6$ or $V8$ or IT in the inferotemporal cortex. The cells in A have in general large receptive fields allowing them to integrate correlations. Our hypothesis is that these cells can adapt their activity to a specific global invariance structure described by a finite dimensional Lie groups. For example this group can be the Euclidean group in area OT, the conformal group in $V4, V8, IT$ or the projective group in $V5, MT, MST$. To express this hypothesis, we introduce the sets M_A that represent parameters of the activity of A (cf. 2.4). The vector space V_A describes the degrees of freedom of the response of the area. We also introduce the sets I_a of characteristic cycles of dynamics and their product $\mathscr{I}_A$. *A priori* the activities are functions on the product of $M_A \times \mathscr{I}_A \times V_A$, which is infinite dimensional. However our hypothesis will ask that these activities depend only on the projection to a finite dimensional quotient $M'_A \times \mathscr{I}'_A \times V'_A$. Moreover we will require the existence of a Lie group G'_A acting on M'_A, $\mathscr{I}'_A$ and V'_A, and of a period mapping $\widetilde{P'}$ satisfying the equation of adaptation (7.9) with respect to this group. In particular the hypothesis implies a dimensional reduction in each higher visual area. Remark that, to get sub-sets $M'_A, \mathscr{I}'_A, V'_A$ and residual symmetries G'_A, a natural procedure would consist to introduce systems of differential equations on M_A and $\mathscr{I}_A$, such that M'_A, $\mathscr{I}'_A$ and V'_A are their solutions. These systems should express "association rules" in A.

Note that reduction of invariance to a Lie group G'_A can be accompanied by a large indifference; an example is in the anterior temporal lobe, where certain cells detect only topological aspects of figures (cf. [252].)

The "image in A" itself corresponds to a vector valued function s_A on M'_A, representing the response associated to the element in $\mathscr{I}'_A$ corresponding to the visual input coming through the areas $V1, V2$, and a contextual modulation in $\mathscr{E}_A$. Such a function on $\mathscr{I}'_A$ can be seen as a co-homology class for the space $\mathscr{I}$ that is associated to the primary areas.

We must also consider families of operators that relate different higher areas A and B, to express how different areas interact. These operators are induced by non-linear pseudo-differential operators (of the type introduced in section 2.1), and compatible with the invariance structures. They represent the internal work on the image in the brain. In particular there contain feedback information from A to $V1, V2$; it is known that, even at the first instants of analysis, the primary activations are modulated by contextual effects, and higher recognition through feed-forward precision, horizontal connections, inhibition and feed-back connections. (Cf. [164] for the representation of curvature in $V4$.)

Example 1: in $V4$ or $V8$ a cell can represent a color in a region that takes in account all the colors in $\mathscr{I}$; this resulting color is closer to sensation than the colors in $\mathscr{I}$.

Example 2: in IT a cell can represent a set of parallel lines localized in a strip of the horizontal plane.

Interestingly, the structure of variability in $V1$ and $V4$ are similar ([205]).

3) The next step for modeling recognition consists in describing how the above operators can define more abstract and stable equivalences classes, forgetting about the details in the various representations s_A and giving unity to the "image". We suggest that this step needs a further co-homological construction. Note that the result of this construction is not necessarily new information in other brain areas, it could be that, but it could be more simply a sort of synergy between sensory areas corresponding to a specific distribution of activities in these areas, as described by Hebb (cf. [82], [224]).

An example from Mathematics for this second level of identification is given by the concept of isomorphism classes of geometric objects. For instance for smooth manifolds: at the first level, the notion of atlas on a set X is introduced, an atlas is a covering by compatible charts, then a manifold is defined as an equivalence class of atlases on X; at the second level appear the isomorphism classes of manifolds. But these classes can also be defined as elements in the first co-homology of a sheaf over the category of open sets in numerical spaces with value in the pseudo-group of local smooth isomorphisms; with this road, at first level are co-cycles, at second level are co-homology classes.

A paradigm for the ultimate equivalence relation is the De Rham operator d on differential forms over a smooth manifold (cf. [50]): in this case co-homology classes are forms α verifying $d\alpha = 0$ modulo forms which are $d\beta$. The analog of the condition $d\alpha = 0$ should say that form is a *good form*, i.e. well formed in the sense of Gestalt, the analog of quotient by the elements boundaries $\alpha = d\beta$ should say that perception consists in forgetting something. Note that in the usual case of De Rham the general covariance and the naturality for all manifolds select the operator d among all operators on differential forms. We shall hope that in the case of images, also covariance and naturality would select the wanted "operator d".

Thus we suggest to consider the stabilization of an image as a class for a convenient co-homology, as we have done for internal categorization spaces in section 2.4 (cf. Appendix 1). Consequently the stabilization of an image would appear as co-homology of co-homology because the sets $\mathscr{I}'_A$ were already co-homology spaces. The dimensional reductions to the $\mathscr{I}'_A$ in the higher areas and the final rules of selection by $d = 0$ give together the expression in our model of the Gestalt rules of good formation: *symmetry*, *parallelism*, *smooth continuation*, *proximity*, *similarity* and *closure*. See Spillman and Ehrenstein in *TVN*, [44].

4) Finally for going to object recognition, we suggest to copy the relation of constancy of colors in the Theorem 3.4.1:

$$[SI^1] = A_S R A_S^{-1}[SI^0] \tag{7.128}$$

But now $[SI]$ denotes the equivalence class of the image of the object S, A_S is the deformation operator telling how the object changes the image at the level of classes, and is R the adaptation operator between classes of images, describing the invariance.

However, for objects, there is a necessity to use all sensory modalities, not only vision, and also many other modalities, like motor control. But the above model can be extended to any representation-of-objects, not only visual images, for instance sounds or odors, or motor plans:

Suggestion 5.4.1: 1) a *representation-of-object* is an equivalence class S in a co-homology space of virtual dynamical attractors for a system of brain areas, it is subject to adaptation R in some invariance structure G; 2) an *object-in-itself* (perhaps coming from a physical object in the external world) is an operator A of deformation of co-homology classes; 3) an *object*, as internalized entity, is an orbit for the conjugate group $ARA^{-1}; R \in G$.

7.6 Perspective Today: Information Topology

To understand better the nature of the internal spaces at works in the brain and the invariance structures on them for adaptation, there is a need of principles for a pure dynamic of information.

Several attempts were made in this direction (Barlow 1961, Von der Malsburg 1981, Rolls and Treves, Bialek 1992, Amari, Shompolinski, Nadal, Sejnowski, Friston et al. 2007, 2009, ... see Olshausen in *TVN*). These works started with the research of Schrödinger, "What is life", on negentropy.

An attractive principle is Infomax, postulating that mutual information between the brain and the external world $I(S;E)$ is maximized. However (see Baudot thesis) this principle has to be complemented with an over-complete basis representation in order to account for the sparseness of the code usually observed in the cortex.

One hope is to find evolution rules for the joint probability of neurons that depend on the set of all multiple information quantities (or higher order mutual information, see [47]).

A first step in this direction is to understand the structures that emerge from the distributions of multi-information on a family of probabilities and a compatible family of random variables.

This is what we explored with Pierre Baudot in a series of papers "to be submitted", but exposed in several seminars. Without pretending we solved the problem of writing dynamical equations for adaptation, I indicate in what sense our work could be relevant. Note the cited thesis of Pierre Baudot contained most of the questions and ingredients for this joint work. This thesis linked the theoretical approach with impressive experimental results of Baudot et al. showing the adaptation of probability of responses in $V1$ to higher information in images, for instance the decrease of spike variability for natural images and natural eye motions (also unpublished result in other form than the thesis, but frequently exposed).

Note that many recent works contain similar results, for instance [40], [39], [81], [85].

We found a way to define a kind of geometry and a kind of topology for a set of probability laws and a compatible set of variables. The first idea was to put on an equal footing random variables and probability laws forming the pairs (X,P). The second ingredient was a definition of multi-information quantities; this was achieved by a co-homology theory inspired by the co-homology of groups. Examples of co-cycles are Shannon higher information quantities. Examples of non-zero co-homology classes are furnished by entropy and Kullback-Leibler distance. The third ingredient is the study of convexity-concavity properties of binary multi-information functions.

Most of our computations dealt with probabilities on finite sets, where the probability space is a standard affine simplex, and the set of variables corresponds to a set of partitions of the simplex.

Remark in special cases it is also possible to decompose the Kolmogorov entropy of a conservative dynamical system into higher information quantities. This extends the point of view of higher correlations, in relation to Lyapounov exponents.

In our opinion, the most notable theorem on the distribution of information quantities (close to our approach), was established by Hu Kuo Ting ([215]). It allows to associate already known topological forms to specific information distribution; for instance standard Borromean links are associated to the (negative) minimum of the third order mutual information (Matsuda [139]). Standard Markov chains do not give rise to non-trivial link ([215]).

This constitutes our point of departure: by considering only the information quantities a geometry appears on the set of probability laws. This geometry is organized locally by special subsets of variables (like generalized Borromean links), representing local attractors of the information distribution in the simplex.

Let M denotes a variety of probabilities. The main phenomenon we describe is the appearance of "topological forms" on the collection of random variables, that are stable configurations of part of the variables having singular distributions of information, reminiscent of the Gestalt rules. These forms depend on the probability laws, thus we obtain a kind of geometry on M, given by the change of forms of observation.

We propose that the multiple information quantities of a probability law provide its Gestaltic-shape description. Then special configurations of information distribution, like Borromean links, correspond to the expression of Gestalt rules (as it must be for co-cycles).

Let us come back to the nervous system, or a subsystem, for instance the visual system of mammals.

We must distinguish (as before in the text) between the family of stochastic processes more or less deterministic that constantly exchange energy and information between the system and the world and inside the system, and the family of laws of these processes $\mu \in M$. Thus we propose to identify M with a set of probabilities on the attractors of the neuronal dynamics. This is not so original Cf. Olshausen, [161], [162], Sejnowski [21], [197]. The fact that parameters of activity

of neurons identifies to a space of probability laws is essential in the approach of Amari (cf. [243]); accordingly this gives a differential geometry of information that is related to the geometry of forms of mutual information when statistical methods for large samples are considered, cf. [38]. And we consider the dynamics of adaptation on M. We assume that knowledge on μ comes only from certain variables $X, Y, ...$ These variables have a specific structure (a category of commutative algebras) which describes the possibility of observation. Then the discussion of "forms of information" applies. The ideal space I represents special events, or past events that could be doubtful, or future events with ambiguity; they correspond to observable functions, i.e. random variables. The virtual attractors that are represented in I coincide with the special configurations of the observable variables. It is important to remark that they correspond to physical flows in the brain.

To link this approach with Galois information, or with the compensation equation between M and I that we exposed in this text, we need a natural group G (or a category) acting on the co-cycles. We do not exclude that the probabilistic information structure is sufficient to generate this Galois actions, but we do not know. It could also happen that Galois theory and probability theory belong to a common wider theory. (Note that Quantum probability introduces naturally Lie groups of symmetries as subgroups of the unitary group, and that ordinary finite probability plays with finite subgroups of the symmetric group.) However, in the case of neuronal systems, the one-dimensional *scaling* semi-group must act on I; it contracts space and dilates frequency. We shall assume that this semi-group expends the local entropies of the joint probability of signals expression, and that it is compensated by adaptation on M.

7.7 Appendix 1: Invariance, Catastrophes and Information

7.7.1 Groups and Information

Group theory can be seen as a genuine theory of information, with the same rights as the Shannon theory, for describing structures of ambiguity. This fact would deserve a complete exposition (a text with Martin Devautour is in preparation), however a few words can help to understand the general co-variance appearing in $V1$ and some higher areas. Our aim is to explain how the point of view of groups and geometry (Galois, Riemann, Grothendieck) relates to statistical information theory (Shannon, Fisher, Wiener) and dynamical systems (Thom, Milnor, Smale).

Evariste Galois considered group theory as part of a general theory of ambiguity, which continues to inspire mathematicians today. The main idea of Galois is simple: let a problem to solve be given, then it is often more useful to understand the form of the ambiguity between the possible solutions, than to try to solve by force the equation. Galois considered the case of algebraic equations E in one unknown and he defined a group G of permutations of the solutions, attached to a set of known numbers S (representing the *a priori* knowledge). The definition of G relies on a basic lemma: the functions $F(x_1, x_2, ..., x_n)$ of the solutions of E which can be determined

from the data in S are exactly the functions which are invariant under the action of a certain group G. Thus G measures the ambiguity on the solutions of E, given S. Moreover, Galois described how the group behaves when S is changed: the addition of new data, for instance the knowledge of a solution of an auxiliary equation E', transforms G into a subgroup H of G, reducing the ambiguity. The choices of other solutions of E' change H into conjugate groups gHg^{-1}. Thus we can say that the quotient set G/H describes the *information*, in the sense of Galois, produced by the auxiliary problem E'. The Galois correspondence associates to each subgroup H of G the set of numbers K_H, generated from the solutions of E, which are fixed by H; it establishes a bijection between the subgroups of G and the subfields of K containing the field of numbers k generated by S. It can happen that G/H itself possesses a structure of group, this occurs when H is a *normal* (or invariant, or distinguished) subgroup, which means that for every $g \in G$ we have $gHg^{-1} = H$; in this case we have $gH.g'H = gg'H$. In this case, named Galoisian, we can consider G/H as the ambiguity structure of a new problem.

Poincaré (La science et l'hypothèse, and other books) explained the sensorimotor origin of the group G of the Euclidean displacements: G can be seen as the Galois group of a joint system made by a moving subject S and its environment E.

By definition, in ordinary Galois theory the Galois group G" of a joint KK' of two number fields K, K' of respective Galois groups G, G', over a basis field k, can be identified with the group of pairs (g, g') where $g \in G$ and $g' \in G'$ act on $K \cap K'$ in the same manner (cf. Bourbaki, Algèbre VII). Thus, in our case it is natural to pretend that the Galois group corresponds to pairs of one transformation g of the sensations in S that are induced by motor action and one transformation g' in E, which can compensate reciprocally. As Poincaré said, from the experiment we see that G" is the group of displacements G. The Galois *mutual information* of S and E is defined by the quotient $G_S \times G_E/G$. Note that, in the same way as two random variables X and Y are independent in the probabilistic sense if and only if $I(X;Y) = 0$, the two fields are linearly independent (i.e. KK' is isomorphic to the tensor product $K \otimes K'$) if and only if $G" = G \times G'$.

This approach of Poincaré was implemented on a virtual robot by Philipona et al.. To deduce the Euclidean *space* E from its isometry group Poincaré invoked specific sensors, like finger tips, whose ambiguity is a rotation group. For the visual space we can do the same, using vergence and accommodation, the properties of visual cells sensing a light spot in a place P; their ambiguity inside the group G is the subgroup H_P of rotations around P. Thus the Galois information of the cell is the quotient G/H_P, which is an exemplar E_P of E. The existence of translations inside G guarantees the existence of canonical isomorphisms between two exemplars E_P and E_Q. This is the origin of an objective space around us.

As we see, continuous groups, not only discrete groups, can appear as Galois groups; this is not exceptional in the infinite dimensional setting, for instance in physical Field Theory, seen as generalization of a theory of singularity (as in the study of phase transition). We can expect that every symmetry from a certain point of view becomes Galoisian.

Information theory and ambiguity theory are synonymous: the information measures the reduction of ambiguity.

Aside from Galois theory there exist other theories of information, in particular the well known theory of Shannon, which is based on probability theory. For Shannon the measure of the ambiguity contained in a probability law $\mathbb{P}$ on a set Ω is given by the *entropy* $H(\mathbb{P})$, which, when Ω is discrete, is the expectation of the function $-\log\mathbb{P}(\omega)$. Then the knowledge that can be expected from a random variable X is given by the entropy $H(X)$ of the image probability X_*P. If Y is another random variable, Shannon defined the mutual information of X and Y by $I(X,Y) = H(Y) - H(Y|X)$ where $H(X|Y)$ denotes the average over y of the entropy of the conditional laws $X_*P|(Y = y)$. We also have $I(X;Y) = H(X) + H(Y) - H(X,Y)$. For Gaussian laws the entropy is a constant multiple of $\log Det\sigma$, where σ is the covariance matrix and *Det* the determinant (more intrinsically, $Det\sigma = DiscQ$, where Q is the co-variance quadratic form). Therefore the mutual information is given by the norm of the cross-correlation matrix.

The theorems of Shannon (cf. Khinchin 1957) show that the structures of possible codings of a message rely on entropy computations.

The theories of Galois and Shannon are directly connected when a group G acts on the considered set of probabilities on Ω, for instance if it acts on Ω itself. In general, the higher is the symmetry of the law $\mathbb{P}$ (the subgroup fixing $\mathbb{P}$), the larger the entropy.

There exist other theories of information based on probability, for instance the theory of Fisher (1925, the first in date), studying statistical metrics, the theory of Wiener (1948) studying prediction. All these theories are related to the entropy or its generalization, the Kullback-Leibler distance between two probabilities $\mathbb{P},\mathbb{Q}$ on the same set:

$$H(\mathbb{P},\mathbb{Q}) = -\mathbb{E}_{\mathbb{P}}(\log\frac{\mathbb{Q}}{\mathbb{P}}). \tag{7.129}$$

This is not a true metric because it is not symmetric in $\mathbb{P}$ and $\mathbb{Q}$. But when the considered probability laws depend smoothly on the points in a manifold M, and when $\mathbb{P},\mathbb{Q}$ become close; this formula can be normalized to give a (possibly degenerate) Riemannian metric on M, the "Fisher information metric". In fact this metric was defined in general by Rao (1945): At any point of a statistical manifold of probability laws $\mathbb{P}_\xi$ it is the tensor

$$\mathbb{F}_\xi = \mathbb{E}_\xi(d\ln(\mathbb{P}_\xi)\otimes d\ln(\mathbb{P}_\xi)); \tag{7.130}$$

As we see it is independent of coordinate choices in M, and this general invariance is its main virtue for statisticians. In a coordinate system $\theta_i; i = 1,...,m$ on M the coefficients of the Fisher-Rao metric $\mathbb{F}$ are given by

$$g_{ij} = \mathbb{E}_\theta(\partial_i\ln(p_\theta)\partial_j\ln(p_\theta)). \tag{7.131}$$

The inverse matrix defines a canonical metric on the co-tangent bundle $T^*(M)$, which appears as a lower bound in the Cramer-Rao inequality for any test $\Phi : H \to \mathbb{R}$ of a given function $\varphi : M \to \mathbb{R}$, at any point $\xi \in M$:

$$\mathbb{E}_\xi(|\Phi - \varphi(\xi)|^2) \geq (1 + |d_\xi(\mathbb{E}_\xi(\Phi) - \varphi(\xi))|^2)\mathbb{F}_\xi^{-1}(d_\xi\varphi, d_\xi\varphi). \tag{7.132}$$

Remark that when the test is unbiased, i.e. when for each point ξ we have $\mathbb{E}_\xi(\Phi) = \varphi(\xi)$, the inequality is a universal lower bound on the variance of Φ:

$$\mathbb{E}_\xi(|\Phi - \mathbb{E}_\xi(\Phi)|^2) \geq \mathbb{F}_\xi^{-1}(d_\xi\varphi, d_\xi\varphi). \tag{7.133}$$

Thus $\mathbb{F}$ appears as a limit of possible precision for a measurement. It has been widely used in Neuroscience (Amari, Nadal). In problems with large sets of data, for instance many independent but cooperative neurons, it appears that maximizing mutual information is equivalent to maximizing the Fisher metric (Nadal, ...).

A remarkable fact is that traditional families of probabilistic laws possess large invariance groups. In fact all classical Lie groups appear as symmetry groups for Fisher-Rao metrics (unpublished folklore, but cf. Amari book).

Example: With the natural coordinates $x = \mu, y = \sigma^2$ of a normal law in one dimension the matrix $\mathbb{F}$ is diagonal and its diagonal coefficients are y^{-1} and $(1/2)y^{-2})$ respectively. This is a model of the hyperbolic plane of Gauss, Bolyai and Lobatchevski; its isometry group is the unimodular group $PSL_2(\mathbb{R})$. For Gaussian families in higher dimensions we find the family $PSL_n(\mathbb{R})$.

It is not astonishing that the whole theory of statistics is traversed by the concept of invariance (cf. Lehmann).

Hartley (1928), and Kolmogorov (1933), have proposed that the whole theory of probabilities can be seen as a theory of ambiguity. As Bayes and Boole anticipated, probability furnishes the basis of a general theory of knowledge. We can say the same thing of the group theory, cf. Souriau "The grammar of the world".

However a third mathematical view on ambiguity is given by the study of the dynamics of competition. René Thom held that fundamentally, all information is of topological nature: to him every information is a *form* and "the meaning of a message is a relation of topological nature between the form of the message and the characteristic forms of the receptor (i.e. the forms able to generate an excitation of the receptor) ..." ([212] p. 156)". We shall show that this view completes the two other views, for applications in Neuroscience and especially for the visual system.

Catastrophe theory puts forward a science of morphologies. Its principle is simple: every form expresses a conflict. More precisely, every phenomenon in the world takes place in a manifold W (perhaps of high dimension, including time), and for each point p in W there is a dynamical system $D(p)$ (for rapid evolution) in an auxiliary space $X(p)$ (varying smoothly with p as a fiber bundle), which decides what happens over p. For us, who are interested by neuronal systems, $D(p)$ will represent the rapid neural activity, contributing to the emergence of a form in the brain for the phenomenon at p. (We admit the existence of several time scales of neuronal activity: a rapid one generating spikes for instance and a slower one for modulating the rapid one; note that at the molecular level also, such a dichotomy holds frequently between the rapid dynamics of pathways and the slower dynamics of gene expression.) The *visible forms* in W are generated by the *catastrophe locus* K, which is the set of points p where the dynamics $D(p)$ bifurcates. According to

Thom, only forms that correspond to generic bifurcations having some sort of stability can be identified. For certain dynamics $D(p_0)$ there exists a canonical family, the *unfolding* of $D(p_0)$, parameterized by a finite dimensional manifold U, in which all accidents deforming $D(p_0)$ can be found. We shall consider only this kind of dynamics. Examples are given by some gradient flows on X, their unfolding describes the possible forms of competition between a finite number of attractor points. For instance, if $X = \mathbb{R}$, the potential $\varphi(x) = x^3 + ux$ represents the birth or the death of an attractor, depending on the sign of u, U has dimension 1 and the set K is the point $u = 0$. The potential $\varphi(x) = x^4 + ux^2 + vx$ represents the competition between two attractors, and in this case the set K is a cuspidal curve in the plane U. Cf. figure ....

The competition between attractors is a model of ambiguous situation. A simple link with probability theory can be obtained, by choosing a positive measure of the sizes of the basins of the attractors; once normalized by the total sum, this gives a probability law $\mathbb{P}(p)$ on the finite set $\Omega(p)$ of attractors of $D(p)$, for each $p \in U$; this quantifies the ambiguity.

Let us consider the richer variant where the value of the potential φ is taken into account; for instance, if $X = \mathbb{R}$, we consider $\varphi(x) = x^3 + ux + c$, or $\varphi(x) = x^4 + ux^2 + vx + c$; then we replace the space U by the extended space $\Lambda = U \times \mathbb{R}$. For $\lambda \in \Lambda$ we define X_λ as the subset of X where $\varphi_\lambda(x) = 0$. The discriminant Σ is the subset of Λ where X_λ is singular. Now suppose we consider all that over complex numbers, i.e. replace everywhere real coefficients by complex numbers, and work over the complexification $\Lambda_{\mathbb{C}}$ of Λ (cf. [13]). Then each non-singular level X_λ is retractable on a bouquet of μ spheres that are named the *vanishing cycles*, where μ is an integer called the *multiplicity* or Milnor number. Thus the homology of X_λ is a lattice $I(\lambda)$ in a vector space $I_{\mathbb{R}}(\lambda)$ (resp. $I_{\mathbb{C}}(\lambda)$) over the real (resp. complex) numbers. Arnold et al. in [13] discuss the case where μ is constant. Now, choose an analytic family of volume forms ω_λ on X_λ, the integrals of ω_λ on the tubes generated by the vanishing cycles can be defined along paths in $\Lambda_{\mathbb{C}}$; this gives a *period* map $\widetilde{P}$ from the universal covering $M_{\mathbb{C}}^{\times}$ of the complement $\Lambda_{\mathbb{C}}^{\times}$ of the complex discriminant $\Sigma_{\mathbb{C}}$ in $\Lambda_{\mathbb{C}}$ to the space $I_{\mathbb{C}}^*$ of linear maps from I to $\mathbb{C}$ (cf. [127], [221]). If we now take into account the real structure, depending on the connected component of the point λ in $\Lambda^{\times}$ (the complement of the real discriminant Σ in the real basis Λ), certain vanishing cycles are real other while others are complex conjugates. For convenient forms ω, the image of the real part $\Lambda^{\times}$ by $\widetilde{P}$ describes a real vector subspace $I_{\mathbb{R}}$ in $I_{\mathbb{C}}$ ([128]). In particular, every generic minimum of φ defines a real vanishing cycle, which is a regular level near the minimum. For some λ the period map for the minima of φ, once normalized, coincides with a probability law $\mathbb{P}_\lambda$.

The following picture is due to Looijenga [127] for simple singularities (i.e. when the unfolding contains only a finite numbers of inequivalent functions) and to Saito [196] and Varchenko [220] in general. First suppose X of odd dimension and the singularity simple; then the ambiguity of $\widetilde{P}$, i.e. the existence of different values for different paths joining the same points, is given by a finite group G (Looijenga, cf. [13], [22]). Moreover, the quotient of $\widetilde{P}$ by G gives an analytic morphism from $M_{\mathbb{C}}^{\times}$ to the quotient of $I_{\mathbb{C}}$ by G: this morphism corresponds to an isomorphism from $\Lambda_{\mathbb{C}}$ to $I_{\mathbb{C}}/G$, sending the discriminant $\Sigma_{\mathbb{C}}$ onto the quotient by G of the set $H_{\mathbb{C}}$ made

by the cycles which have non-trivial isotropy under G (i.e. which are invariant by some $g \neq Id$). Thus the discriminant is isomorphic to the quotient a finite union of hyperplanes. Finally in the simple case, Looijenga proved that each component of the complement of the *real* discriminant Σ in the real extended unfolding Λ corresponds to a finite union of real copies of $I_{\mathbb{R}}$ disposed inside $I_{\mathbb{C}}$; these real copies correspond to linear combinations of minima equipped with special phases.

In the general case of the universal deformation of an holomorphic function with isolated singularity, Saito (cf. [196]) defined the notion of *primitive form* ω_λ, and for such forms established that the period mapping extends to a surjective morphism also generically one to one from $M^{\times}_{\mathbb{C}}$ to $I^{*}_{\mathbb{C}}$. Note that the space of primitive forms for a joint sum of simple singularities has finite dimension; in general the dimension of the space V of primitive forms behaves additively under joins. Thus the best thing in the general case is to consider not only one period mapping but a vector of period mappings, i.e. $\widetilde{P}; v \in V$.

Remark: the origin of the above theory was in theorems of Brieskorn, Grothendieck, on the equations of maximal unipotent orbits of simple Lie groups, showing that continuous groups are also related to the picture.

7.7.2 Homological Forms

Based on these results, showing the compatibility of the points of views of Galois, Shannon and Thom on what is called ambiguity, and information, we suggest a generalized picture for neuronal systems:

Let A be a brain area; a real smooth manifold M_A (playing the role of the covering $M^{\times}_{\mathbb{C}}$ or a subset that corresponds to reality conditions) is used for parameterizing the stable joint receptive fields in the area A, i.e. the way the activity in the area is prepared to change under the influence of the external world or the afferent areas, taking in account the intrinsic properties of neurons in A and their interactions (for instance through interneurons or glial cells). Thus a point μ in M_A represents a certain dynamical system ξ_μ in an internal space X_A (giving a model of the possible responses of A, from molecular events to spikes). Boundary conditions are described by an auxiliary space E_A.

The complete details of the dynamics of the assembly of neurons are not essential to give a definite form in the brain for the external phenomena; for each μ only a stable skeleton I_μ issued from ξ_μ does matter. We assume that all the topological information in ξ_μ is coded by the set I_μ, which we shall call the *vanishing homology* (or simply the homology), whose elements we name the *vanishing cycles*. The homology I_μ represents the way A categorizes the responses when it is in the state μ. This skeleton is defined up to deformation; it has a discrete nature, thus we assume that over M_A it is possible to follow I_μ and identify it with a fixed set I_A.

The set I_μ is issued from a subset Ω_μ it contains, which collects possible attractor regimes of ξ_μ and from memory or context or anticipation, providing ambiguity. We can think to an element of I_μ as a virtual attractor with a phase, like inhibited regimes; only a subset of the phases gives real attractors, belonging to Ω_μ.

The output signal going from A depends on a $\sigma \in I_A$ and a $\mu \in M_A$. A family of probability laws $\mathbb{P}_\mu$ is assumed to be given on Ω_μ, for describing the law of spiking activity in A. Let us denote by I^* the space of numerical functions on I, and name it the *vanishing co-homology* (or simply the co-homology); when we want to specify the coefficients of functions we note $I^*_{\mathbb{R}}$ or $I^*_{\mathbb{C}}$. And let us denote by V^* the space which parameterizes the output dimensions (it plays the role of the dual vector space of the the space V of primitive forms of Saito). We assume the existence of a map $\widetilde{P}$ from M to $I^*_{\mathbb{C}} \otimes V^*$, such that, for any μ and $\omega \in \Omega$ we have $P(\mu)(\omega) = \mathbb{P}_\mu(\omega)$. We name $\widetilde{P}$ the *period map*.

Now a group $\widetilde{G}$ acts on M, and also acts on I, in such a manner that, for any $\mu \in M$, $\sigma \in I$, $g \in \widetilde{G}$, we have

$$\widetilde{P}(g.\mu)(\sigma) = \widetilde{P}(\mu)(g.\sigma). \tag{7.134}$$

This relation expresses the compensation of a change of the parameter μ by a change in the internal state σ. This compensation corresponds to an *adaptation*: a flow in M changing the parameters of the neurons to compensate a change in context.

Note that the brain area A can be composed of many neurons a, each of them has dynamics $\xi_{a,\mu}$ parameterized by a manifold M_a and having homological skeleton $I_{a,\mu}$; the manifold M_A associated to A is a sub-manifold of the joint of the M_a over all the cells a, the space I_A is the product of the I_a, and the vanishing co-homology I^* is embedded in the tensor product of the $I^*_{a,\mu}$ over a. In general the group G acts on I^* but not on the individuals $I^*_{a,\mu}$. Let us nor forget that M is much larger than the set of union of the M_a over a; it parameterizes the interactions between dynamics and not only marginal dynamics.

The response of the area A to a stimulus φ is assumed to be given by the value of $\widetilde{P}$ at a cycle σ that depends on φ and the context ε:

$$\rho(\mu, \varphi, \varepsilon) = \widetilde{P}(\mu)(\sigma(\varphi, \varepsilon)). \tag{7.135}$$

It depends on time t through φ and ε and μ. Note that ρ is a vector in V_A^*; to get scalars we must consider $v \in V_A$ and take the bracket $\langle \rho, v \rangle$. This is an important point because the output of a brain area is a field of responses of neurons, in general not reducible to a scalar function.

The group $\widetilde{G}$ describes the ambiguity of the period map on the quotient $M/\widetilde{G}$. Its action on I^* defines the Galois group G of the system. We see that, for each v in V_A, the map $\widetilde{P}$ induces a map from the quotient $M/\widetilde{G}$ to the quotient I^*/G. To conform with catastrophe theory we can require the inverse of this correspondence to extend to a bijection from I^*/G to a completion Λ of $M/\widetilde{G}$.

With respect to the inputs, the space I^* creates an internal space with a new geometry, described by G. This space represents the external world, but at the same time, it invents the observable properties of this world.

The intelligible forms according to Thom come from the prolongation to the set Σ of unstable dynamics; this corresponds in I^* to the subset Δ where the isotropy, describing the structure of indetermination, is non-trivial. The full dynamics of X, Λ, I^*

permits to give precision an intriguing observation of René Thom about the human brain ([212] XIII.3). "... in the human brain was realized a dispositive simulator of the self-reproducing singularities of epigenesis, which permits, in presence of a catastrophe of internal space Y and unfolding U, to send the unfolding U in the internal space Y, realizing the confusion between internal and external variables." (See also [214]) What we have suggested in the present text, is that, first this confusion is not reserved to humans, but it appeared in all living entities, and second, this confusion is ambiguous, in the sense that the correspondence between neural processes and thoughts contents is multi-valued; the ambiguity structure being the place where symmetries are invented.
The homological skeleton adds ambiguity to the output with respect to the input.

The prototype of $\widetilde{G}$ is the group of rigid motions, it first appears as a Galois group, describing the ambiguity between what moves in the world and what results from body's movements, then it is imposed as a geometry on the world, for isotropy and homogeneity, that do not exist in reality, but help perception. An example of a system where this group appears explicitly in the entry is the parahippocampal region cf. section 5.3.
To summarize the invariance expressed in a given area A, we start with the group collecting the transformations of the environment E that have no effect on the responses in A; this is the *indifference group* written $G(E)$. Next we have a group $G(I)$ acting on the quotient $I = E/G(E)$ representing categories in A, and a group $G(M)$ acting on the set M of parameters describing the possible dynamics M; a subgroup $\widetilde{G}$ of the product $G(I) \times G(M)$ is made with the transformations that have no effect on the response; from the above discussion we could name it the *ambiguity group*, or the *adaptation group*. The full group $G(I) \times G(M)$ acts on the response space R, thus the notion of co-variance of the response applies to this group.

7.8 Appendix 2: Unitary Representations

Harmonic analysis permits to describe how discrete units can work with continuous symmetries.

References: [222], [110], [83].

Suppose G is a Lie group and choose a left invariant measure on G (named Haar measure).

A unitary representation is a morphism $g \mapsto U^\lambda(g)$ from G to the group U_λ of bijective isometries of a complex Hilbert space H_λ; the representation is said to be irreducible when any invariant subspace of H_λ is $\{0\}$ or H_λ itself. See [110].

Definition: For any integrable function $\phi : G \to \mathbb{C}$ we define the Fourier-Plancherel transform by the equation

$$\widehat{\phi}(\lambda) = \int_G U^\lambda(g)\phi(g)dg \tag{7.136}$$

where λ describes the set $\widehat{G}$ of unitary representations of G. Then $\widehat{\phi}(\lambda)$ is an operator, an element of U_λ.

In what follows we assume that the Haar measure dg is also invariant by right translations in G. When such a measure exists the group is said to be unimodular. Any compact group, any discrete group, any commutative group is unimodular. The affine group (see 2.1), is non-unimodular. The Lie groups of interest for us, the Euclid group (displacements) and the Galilean group are non-compact but they are unimodular. Other non-compact examples are semi-simple Lie groups (cf. [83]), or nilpotent Lie groups (cf. [110]).

The Plancherel Theorem, valid for any unimodular Lie group, asserts the existence of a measure $d\pi(\lambda)$ on $\widehat{G}$, such that for any square integrable function ϕ on G, which is also integrable, we have

$$\int_G |\phi(g)|^2 = \int_{\widehat{G}} Tr[\widehat{\phi}(\lambda)^* \widehat{\phi}(\lambda)] d\pi(\lambda), \tag{7.137}$$

and the inversion formula holds true:

$$\phi(g) = \int_{\widehat{G}} Tr[U_\lambda^*(g)\widehat{\phi}(\lambda)] d\pi(\lambda) \tag{7.138}$$

The proof of this theorem for finite groups is due to I.Schur, for compact Lie groups to H.Weyl, and the general case of unimodular separable locally compact groups(in particular Lie groups) is due to Mautner and Segal (cf. [37]). The coefficients of the irreducible unitary representations have strong orthogonality properties (cf. [83]), but they rarely form a generating system of square integrable functions on G; for compact groups they do.

We suggest that the coefficients of unitary representations of a group G are good candidates for describing the receptive fields of neurons that are modulated by trajectories in G. This requires a definition of "windows in the groups", generalizing domains in the visual plane that can generate spikes.

Given a distribution μ on G depending on time t, and a smooth function ϕ on G, we define the translation operation on distributions by

$$\langle \tau_t(\mu), \phi \rangle(s) = \langle \mu, \phi \rangle(s-t),$$

and the inversion operation on distributions by

$$\langle \mu^\vee, \phi \rangle = \langle \mu, \phi \circ \varsigma \rangle,$$

where $\varsigma(\phi)(g) = \phi(g^{-1})$.We also write $\varsigma(\phi) = \phi^\vee$.

The first ingredient of a *simple window* c is a pair (σ_c, K_c) of one sigmoidal function from $\mathbb{R}$ to $\mathbb{R}$, and one C^∞ function on G, such that activity of c at time t induced by a stimulus μ is (at least in part) explained by the formula

$$R_t(\mu) = \sigma_c[K_c * (\tau_t \mu)^\vee]. \tag{7.139}$$

In general we will suppose that K_c respects causality, implying that R_t depends on the restriction of μ to values of s before t. When μ is a function we obtain

$$K_c * (\tau_t \mu)^\vee = \int_G dh K_c^0(hg_0^{-1}, s)\mu(h^{-1})(t-s).$$

In the case of a unimodular group, this also gives

$$K_c * (\tau_t \mu)^\vee = \int_G dh K_c^0(g_0 h^{-1}, s)\mu(h)(t-s).$$

In the hope of maximizing invariance and information together, we take a function $K_0(s)$, like a Gaussian density, centered on the identity element of the group G, and we choose an irreducible unitary representation $\lambda(s)$, and two vectors $\psi_1(s), \psi_2(s)$ in the Hilbert space $H_{\lambda(s)}$. The function K_0 gives the *size* to the window, the representation λ generalizes the preferred *frequency*, and the vectors ψ_1, ψ_2 generalize the phase. Then we define

$$K_c^0(g,s) = K_0(g,s)\langle \psi_1(s)|U^{\lambda(s)}(g)|\psi_2(s)\rangle,$$

so we obtain the following generic formula for the elementary linear operators underlying the receptive fields:

$$K_c * (\tau_t \mu)^\vee = \int_{\mathbb{R}} ds \int_G dh K_0(g_0 h^{-1}, s)\langle \psi_1(s)|U^{\lambda(s)}(g_0 h^{-1})|\psi_2(s)\rangle \mu(h, t-s)$$

The corresponding receptive fields could be named *harmonic receptive fields*.

In [24], we suggested that the elementary windows associated to the Galilean group are well adapted to describe non-linear receptive fields of the vestibular system. A subgroup G_0 of the Galilean group is isomorphic to the Euclid group, $E(3)$ of displacements in $3D$ Euclidean space. The unitary representations of G_0 were determined by the induction method of Mackey (1958). See also Thoma (1958), Ito 1952,1953, Mackey 1952,1953, 1958.

The sequel of this work, aimed at studying the grouping of the harmonic receptive fields, is the current thesis of Alexandre Afgoustidis.

Example: In two-dimension, for the Euclid group $E(2)$, the representations come in two families. First, the *special representations* are described by a relative integer number N, they are of dimension 1 and see only the rotation part in g.
Second, the *generic representations* are classified by a positive real number ρ, the Hilbert space is the space of square integrable functions on the circle; the transformation $g(\mathbf{a}, \alpha)$, whose parameters are the rotation of angle α around 0 and the gliding of velocity $\mathbf{a}$ of modulus r and argument φ, is represented by

$$U^\rho(g)(f)(\theta) = e^{i\rho r\cos(\theta-\varphi)} f(\theta-\alpha) \tag{7.140}$$

The coefficients in this case are associated to the canonical Fourier basis $\exp in\theta$; they give the following functions on G

$$t(g) = \langle \psi_1 | U(g) | \psi_1 \rangle \tag{7.141}$$

That are

$$t^{\rho}_{mn}(g) = i^{m-n} e^{-i(n\alpha+(m-n)\varphi)} J_{m-n}(\rho r) \tag{7.142}$$

See [222].

In this model we obtain the following formula for describing the response to a periodic stimulus ω in a direction θ:

$$R(t) = \int k_0(s) ds \cos(m(\theta - \theta_0)) J_m(\rho_0 \cos(\omega(t-s)); \tag{7.143}$$

where J_m denotes the Bessel function with integer index m.

Definition: in general the Bessel function of index t in $\mathbb{R}$ is given by

$$J_t(z) = \sum_0^{\infty} \frac{(-1)^n (z/2)^{2n+t}}{n! \Gamma(n+t+1)}. \tag{7.144}$$

It is a solution of the Bessel equation

$$\frac{d^2 y}{dz^2} + (1 + \frac{1-4t^2}{z^2}) y = 0 \tag{7.145}$$

At the first order approximation in ρ_0 this gives:

$$R(t) = \rho_0 \int k_0(s) ds \cos(m(\theta - \theta_0)) \cos(\omega(t-s)). \tag{7.146}$$

When k_0 is of Dirac type Dirac, $\delta(t - t_0)$, we find the classical model:

$$R(t) = \rho_0 \cos(m(\theta - \theta_0)) \cos(\omega(t - t_0)). \tag{7.147}$$

However, when k_0 is a real Riemann-Liouville derivative of order D_0, we find a "dynamical response":

$$R(t) = \rho_0 \omega^{D_0} \cos(m(\theta - \theta_0)) \cos(\omega(t - t_0')). \tag{7.148}$$

We recover the known characteristics of a central vestibular cell, which are the gain ρ_0, the phase delay t_0' and the dynamical index D_0.

In the $3D$ space, for the generic series, the Hilbert space is a convenient subspace H_λ of the space H of square integrable functions on the orthogonal group $O(3)$. We fix a number ρ, and a vector $\overrightarrow{e_0}$ of norm 1; then, if g is the composition of the rotation R centered in 0 withe Galilean gliding of constant velocity $\overrightarrow{v}$, we define

$$U^{\rho}(g)(f)(S) = e^{i\rho \overrightarrow{v}.S(\overrightarrow{e_0})} f(R^{-1}S) \tag{7.149}$$

Cf. [222].

The modification of the response due to space effects consists in replacing the circular function $\cos(m(\theta - \theta_0))$ by a spherical harmonic and the Bessel function of integer index by a Bessel function with semi-integer index.

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