# Neuroconstructivism: a developmental turn in cognitive neuroscience?

## I

## Introduction

Since its birth, brain science has been for the most part the study of the structure and functioning of a brain already formed, the study of the endpoint of a process. Brodmann areas, for instance, are cortical areas of the adult brain (Brodmann, 1909). In his authoritative *Neurobiology*, Shepherd devotes only one chapter (out of thirty) to developmental neurobiology (Shepherd, 1994). From early attempts at functional localization by Gall or Broca to recent neurocognitive models like the model of visual cognition proposed by Milner and Goodale (Milner & Goodale, 2006), functional decomposition of the brain essentially remained the decomposition of the brain of the adult. Neuroconstructivism, then, as it has been recently vindicated (Mareschal et alii, 2007; Sirois et alii, 2008) could be understood, first, as the idea that we should take brain development more seriously. This suggestion comes at a time when in many fields of biology, ontogenetic development has become the object of both fascinating discoveries and intense speculation. But there is more to neuroconstructivism than a developmental perspective on the brain, as it can be understood as a view of cognition: it is this view of cognition that motivates a specific, renewed approach to the human brain. What neuroconstructivism is challenging, in fact, is a view of cognitive *explanation*, and of cognitive *development*.

The view of cognitive explanation it rejects is in part derived from the idea that Marr expressed when he said that we should not begin by the study of feathers if we want to understand bird flight (Marr, 1982). It is the idea of independent levels of investigation, the idea that psychological explanation is, in principle, fruitfully divorced from the study of low-level implementation. Neuroconstructivism suggests a view of cognitive explanation where there is no point to the separation of levels. There is no such separation in practice, because neural events are causally relevant to the understanding of cognitive development in its many forms, both typical and atypical. And there is no such separation in another sense, because investigation at different levels (levels being this time: the cell, the brain, the whole body) may rely on the same kind of explanatory factors. As "mechanisms" of the same kind operate at different levels, explanations in different fields are fundamentally of the same type. The unity of cognitive research, then, is not obtained via the existence of a discipline that would shape the whole field (e. g., evolutionary psychology, seen as a guide to neuroscientific research) but through the use of recurring patterns of explanation. And as neuroconstructivism adopts as its highest "core" principle the principle of "context-dependence"[1], brain is not the largest unit, the largest containing system that it considers. Even the brain in development and its changing abilities have to be contextualized. This is why neuroconstructivism perceives itself as the convergence of the work in different disciplines and trends of research, namely: developmental neurobiology (the study of "encellment" – see Shepherd, 1994, chapter 9); developmental cognitive neuroscience (the study of "enbrainment" – see Johnson, 2005a); developmental embodied cognition (the study of "embodiment" – see Thelen and Smith, 1994).

[1] Mareschal et alii, 2007, chapter 5; Sirois et alii, 2008, p. 325, and figure 1 below, section III.

The view of cognitive development it rejects is the view that cognitive abilities are highly canalized biological features[2], i.e., features that develop in a similar fashion in widely different environments, and are essentially insensitive to environmental variation. In contrast, neuroconstructivism also suggests a view of cognitive development that is highly sensitive to events in both internal and external environments. It rejects a deterministic view of epigenesis and rejects a view of cognition where inborn abilities would simply unfold in time. Brain development matters, in this sense, not just because there is no preexisting, detailed blueprint of its organization - because, for instance, the 'protomap' view of the cortex (Rakic, 1988), where the identity of any cortical neuron can be traced back to the specific spatio-temporal circumstances of its formation in the proliferative zone, has now been abandoned (Sur and Rubenstein, 2005). Brain development matters because we may learn from it, not only about the adult brain, but about how we acquire our own mental powers, and what constrains a child's typical or atypical cognitive development.

I do not intend to comment here on every single aspect of the neuroconstructivist program, such as the importance it gives to computational modeling, or its endorsement of the embodied cognition view. My first goal is to provide an understanding of the reasons why neuroscience may need such a program– which gaps it is supposed to fill, which inferences it challenges. I shall therefore focus on early critiques of inference from functional commitment specialization of cortical areas to their inborn specialization (II), and on the link between the controversy over plasticity that arose in the 1990s and the current neuroconstructivist model of brain development (III). My second goal is to examine the core of the program itself, its guiding "principles" – that is, the principle of context-dependence and the idea of level-independent mechanisms (IV). I suggest that such a program, as it stands, suffers from both under-determination and over-generalization (V). Because of these defects, and because developmental neuroscience has not been the main concern of philosophers who analyse neuroscience in terms of mechanisms, a dialogue between neuroconstructivism and the philosophy of neuroscience may yield mutual benefits (VI).

## II

## The broader context: the Wundt-Munk controversy about the origins of brain function

The anti-nativist stance of neuroconstructivism can be situated in its opposition to recent Chomskyan, Fodorian, or massive modularity views about neurocognitive explanation. But it has roots in more ancient debates that are worth mentioning. One reason is that there are good reasons to prefer a continuist view about the history of cognitive neuroscience over a discontinuist one. Even if the expression "cognitive neuroscience" itself has not been widely used until recently, what this expression refers to may be seen a research program that finds its origins in the 19th century, and whose development can be understood as the application to the brain of these heuristic strategies that Bechtel and Richardson have called decomposition and localization (Bechtel and Richardson, 1993). The central idea in this program is that the discovery of brain mechanisms is key to the understanding of the corresponding mental powers. Notable differences in investigation methods, scientific tools and intellectual background notwithstanding, privileging continuity should not be controversial, as many topics that belong today to cognitive science were treated in the 1880's by scientists like Meynert, Munk, Ferrier, and Jackson. One of the first philosophers to have taken the measure of such a program was Wundt in his *Elements of Psychophysiology* (Wundt, 1880). In this monumental work as in related papers, his aim was to make explicit the founding principles of such a science, to sum up its main discoveries, and to offer critical views about some of its central claims. The critical views were meant

[2] Ariew, 1996.

as a positive contribution to a young domain of investigation. Researchers like Munk, according to Wundt, offer only a mixture of important scientific discoveries and old prejudices. Making these prejudices explicit is a means to an end: clearing the ground for further questions and investigations. In order to achieve this, Wundt sketches what we may call a constructivist answer to nativist views.

Wundt does not reject the principle of localization of function within the brain, a principle that is central to the mechanistic methodology of brain science. But he thinks that the kinds of methods used by neuroscientists may lead them to adopt views that are not, in fact, supported by available evidence. First, the localization of lesions should not be conflated with the localization of functions. Focal lesions in pathological cases are signs of the involvement of brain regions in cognitive tasks, but they do not, by themselves, indicate what the exact nature of this involvement may be. Second, and more importantly, evidence of localized functions is not evidence of inborn commitment of brain areas to perform definite functions. To the old holistic error (no functional decomposition of the brain is possible, or fruitful) we should not substitute what Wundt calls the phrenological error (Wundt, 1891): the claim that each part of the brain has its own, immutable, pre-specified function. In order to reject phrenology, according to Wundt, it is not enough to give up the entire list of mental faculties as they were defined by Gall. Quite strikingly, Wundt sees (much before Fodor, but for opposite reasons) that there is more to Gall than a set of old prejudices that everyone has already overcome. There is a mixture of nativism and what we would call modularity (that is, functional specificity of largely autonomous units or powers, units that may be localized in the brain) and this mixture, in 1880, according to Wundt, still provides the framework of much scientific work done in brain science. This point: no sound inference from functional specialization in the adult brain to inborn commitment of the corresponding brain parts) is central to Wundt's proposal. The task of "physiological psychology" (roughly, our cognitive neuroscience), as it is defined by Wundt, is not only to establish what functional localizations are, but more importantly, *where they come from*. Nativist views, according to Wundt, are just the product of our ignorance in this matter. The first part of Wundt's work, then, is to explain why the nativist view of inborn commitment of brain areas should be rejected. To this end, Wundt relies on recent work on neural plasticity. Brain function, when abolished by the destruction of some quantity of brain tissue, may be spontaneously restored during recovery. This is explained, according to Wundt, by other neural elements "taking over" the defective ones. This shows that with different connections, different input/ output conditions, functional specificity of brain components may be altered. The possibility of a substitution of one nervous element to another is evidence against strict preexisting definition of specific neural function. This principle of "Ersatz" function itself falls under another, more general principle that Wundt calls the principle of adaptation: "any central element is adapted to its function as it has to perform it more frequently under the pressure of external conditions"[3]. Plasticity, then, when it is linked to physiological recovery after brain damage, is not a *sui generis* phenomenon: it is just an extreme case of adaptation as defined in this broad sense[4]: in this case, "being progressively adapted" does not mean doing something better with time (improvement of performance, as in a Jamesian definition of plasticity[5]) but being able to alter one's pre-existing function under external (contextual) influences. But Wundt does not stop there. He asks: why is this principle of adaptation valid? Where does the power of neural elements to adjust to external circumstances come from? And his answer is: it comes from the lack of specific functional commitment of central, neural elements at birth. If the definition of function is the *result* of the process of brain organization, then it is not *that* remarkable that neural elements may change their functional role in special circumstances during adult life. It is just that no "restriction of fate" during life, no

[3] Wundt, 1880, Part I, chapter V, 7: General principles of central functions.
[4] A strikingly similar view is expressed in Elman and alii, 1996, p. 247-248.
[5] James, 1890.

special adaptation leads to a unique, non-reversible functional commitment. Evidence of plasticity brings back to the necessity of a scientific explanation of the outcome of epigenetic processes. Nativism, then, is not a solution to the problem of the origin of functional specialization within the brain, it is just a way to ignore it[6]. Plasticity depends on the adaptive power of neural elements, which itself derives from the fact that their standard, domain-specific activity during adult life should be seen as the temporary, reversible product of the changes imposed by brain organization (for instance, input and output conditions) on initial, non-specific response properties of neural elements. The fact that Wundt has little to say about the detail of these changes makes his clear, synthetic view of this cluster of important questions even more remarkable.

## III

### The debate on the significance of neural plasticity for the controversy about representational nativism.

Just as Wundt once challenged a phrenological view of inborn functional determination, constructivists have challenged a deterministic view of brain development one century later. The intellectual debt of the co-authors of *Neuroconstructivism* towards Jeffrey Elman, Annette Karmiloff-Smith and the other co-authors of the manifesto, *Rethinking innateness*[7] is obvious enough. What is needed in order to understand neuroconstructivism is rather to clarify the meaning of the shift of emphasis from the analysis of neural plasticity (considered in 1996 as evidence against representational nativism) to developmental cognitive neuroscience as it flourished in the following years. This can be done through the debate between the philosopher Richard Samuels and the co-authors of *Rethinking innateness*[8]. Samuels holds that Elman and his colleagues have misinterpreted the neurobiological facts: neural plasticity does not, contrary to their claims, falsify representational nativism. O'Leary and Sur, in a striking series of experiments, offered evidence that in the brain of mammals, the sensory cortex of a given region may take response properties of another region under exceptional circumstances. Studies have shown that fetal neurons taken from the "visual" area may come to exhibit the organizational and functional properties of the neurons of the somatosensory region where they have been transplanted (O' Leary and Stanfield, 1989). Rewiring experiments have also shown that the somatosensory cortex of ferrets, when it is deprived of its normal input, and when it receives visual inputs early in life, may develop response properties that are typical of the "visual cortex" (Sur, Pallas & Roe, 1990). Are we to think, then, that parietal regions that are usually described as 'somatosensory areas' are not intrinsically dedicated to the representation of somatic states? According to Samuels, neural plasticity has no such implications. First, innate properties are not necessarily intrinsic properties (that is, properties that are non-relational). If representational properties are extrinsic, rather than intrinsic properties, representational properties of a given set of neurons may both be innately specified and depend on the relation of these neurons to the rest of the cortex and to the environment. In this case, when we are modifying the input conditions of these neurons, it is no surprise that their representational properties are altered. Samuels thinks that constructivists suggest mistakenly that nativists have to adopt an Invariance principle such as

[6] For instance, Wundt sees very clearly the implications of a constructivist view for a question like the « specific energies of nerves » inherited from Müller, a problem that had become in his days the problem of the relation between sensory *qualia* and brain regional activation. For him, there is no individualistic, internalist explanation of the differences between sensory modalities. The supervenience base of visual experience cannot be the activation of the "visual" region of the brain alone, independently from the nature of sensory input.

[7] Elman & alii, 1996.

[8] Samuels, 1998.

The innately specified (representational) properties of a piece of cortical tissue T are invariant under alterations in T's location within the brain and alterations in the afferent inputs to T.

But Samuels thinks that because of the distinction between intrinsic and innate properties, nativists do not have to accept this Principle. Moreover, they are, in fact, committed to what he calls Organism nativism rather than Tissue Nativism. Tissue nativism is a claim about representational properties of specific brain parts. Organism nativism is a claim about inborn cognitive abilities of whole organisms or people and it is entirely independent from claims about innate commitment of brain parts or specific localization of function. Even a refutation of tissue nativism (a refutation that, according to Samuels, experiments on plasticity do not provide) would not be a refutation of representational nativism in general.

Let's focus on tissue nativism, as it is linked to the definition of the functions of brain parts, and as Samuels holds that it can be vindicated against Elman's views. First, innate specification of representational properties is difficult to reconcile with some existing neurophysiological data. The crucial role of the activity of visual areas in blind subjects during Braille reading seems to support a view of sensory areas (the "meta-modal organization" of the brain) where they possess a "purpose general" ability to treat incoming sensory signals rather than an inborn commitment to treat one or another kind of such signals[9]. In the case of Braille reading by blind subjects, response properties of the so-called "visual area" are different from what they are in standard cases, without any transplant or re-wiring. In congenitally deaf mice, it has been shown that some neurons of the auditory cortex develop responses to visual and somatosensory stimulation, and that the response properties of other regions, like the visual cortex, are themselves altered (Hunt, Yamoah and Krubitzer, 2006). What evidence do we have, then, of an innate specification of the representational properties of visual or auditory cortex, and why would we prefer this nativist view to the parsimonious alternative of a lack of the inborn functional commitment of sensory areas? Second, we can ask ourselves what it means for the representational property of a given set of neurons to be "innately specified". Extrinsic properties, says Samuels, are constitutive of representational properties. But extrinsic properties are defined *during* epigenesis and as *the result of* the specification of neural paths. In this case, how could representational properties be innately specified *before* the outcome of this epigenetic process or *independently* of it? How could they have a pre-existing, definite *content*? And if they don't, how could they exist at all? What is called the "innate specification of the representational property of visual neurons" seems to be a convoluted way of saying that neurons of the striate cortex have early in life a higher *probability* to receive visual *inputs* than, say, somatosensory inputs. Calling this an "innate representational property" conflates different levels: it re-describes a frequent but non-necessary correlate of the outcome of a *neurobiological* process as what is (at the *representational* or psychological level) 'meant to be'. However, defeating a nativist critique of conclusions drawn from plasticity experiments is one thing; explaining where the typical organization of the brain of mammals comes from (especially, the existence of discrete units like cortical areas, and their functional specialization) is another. Neuroconstructivism could be understood as the empiricist answer to the objections made by Samuels to the argument from plasticity against innate specification of representational properties of given brain parts. What is needed is not only manipulations that experimentally alter the extrinsic properties of cortical areas, but an understanding of how functional

[9] Pascual-Leone and Hamilton, 2001. The meta-modal organization hypothesis takes a middle ground in the debate on domain-specific or domain-general abilities of neuro-cognitive systems. It does not involve any claim of equipotentiality of brain regions, but rejects an inference from specialization of a sensory region to a specific domain to an inborn commitment to this specific domain.

specialization and extrinsic properties are specified during brain's development. This is what neuroconstructivism hopes to provide.

## IV

## Neuroconstructivism at work

One way of presenting the neuroconstructivist view may be to begin with the contrast between two theories of biological functions in the philosophical literature: one is the etiological view –functions are nothing but effects selected during biological evolution (Neander, 1991), the other is the systemic view of Cummins: the function φ of a component x in a system S is its contribution to the explanation of the ability of S to ψ (Cummins, 1975). Although it is fairly uncontroversial that in brain science, research is aimed at discovering Cummins functions, and that neuroscience textbooks provide information about the contribution of activities and/or components to larger systems, some still maintain that where there is no history, there is no function (Jacob and Jeannerod, 2003), and that we should consider the functions of brain components as products of evolution by natural selection. I don't want to discuss here the merits of these philosophical views, but rather to point out that we have to take in consideration the finesse of grain of our analysis. For instance, the ability of place cells in the hippocampus to contribute to the formation of maps of the environment (O' Keefe and Nadel, 1978) can be seen as (one of ) their function (s), and what we mean by that may be that it is a product of a certain evolutionary history where natural selection has played a role. However, the ability of these cells to contribute to the individual's knowledge of *his* environment requires more than the existence of these cells and the corresponding history of the species; it requires a certain kind of individual history where *tokens* of place cells end up coding for specific places. An explanation of *actual* orientation of a given individual will require a causal analysis where specific activations of place cells contribute to the ability of the hippocampus to form a map of *his* familiar environment: no actual orientation is provided by past selection for places cells *as a type*. This means that *different* interesting stories may be told about the origin of functions and that one of them may be about their ontogeny. In this sense, developmental cognitive neuroscience and neuroconstructivism fill a gap. They require that we address additional questions that are left unanswered by the evolutionary perspective, and that Cummins' style functional analysis is not meant to solve either:

Question 1: in a given system S, in virtue of what does a component x receive its own power to φ?

Question 2: how did S become able to produce its own, characteristic output? Why ψ (rather than some other activity) in S ?

Developmental Cognitive Neuroscience has to provide answers to these related questions, to give a mechanistic explanation of how components receive the distinctive powers they have. And the idea of neuroconstructivists is that, if we cannot be satisfied with a view where brain development is just brain maturation, we should adopt what Johnson calls the *Interactive specialization view*. To know why component C has received its distinctive role (question 1), we have to look at the developmental history of the System in which C is embedded and at the corresponding external environment. This developmental history causally explains, in particular, the current pattern of connectivity of C and its response properties. To the second question: how does S become able to ψ?, the neuroconstructivist answer is: we can explain the emergence of S's characteristic output ψ through its own interactive specialization and the interactive specialization of its parts. Now to explain of how specialization occurs, constructivism offers a set of *domain-general and level-independent* "mechanisms":

*Competition*: for any given function, neural systems evolve from widespread, aspecific activity to specialized correlates

*Cooperation* : which is another word for functional integration

*Chronotopy*: key aspects of development rely on sequences of events that are closely related: in particular early specialization of a component A constrains the posterior developmental trajectory of a related component B; explaining the latter is impossible without explicit reference to the former.

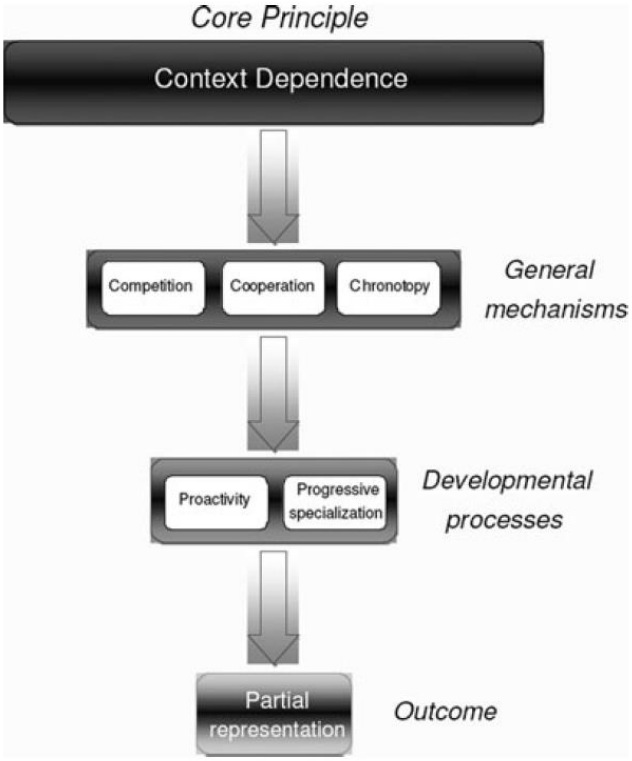


Figure 1. The core principle of the Neuroconstructivist Program

(from Sirois S. & alii, 2008)

Let's take, for instance, face recognition as the *explanandum*. Instead of considering the fusiform area as a cognitive module with an inborn, domain-specific commitment to process face representations, the neuroconstructivist framework invites us, on the cognitive level, to pay attention to the difference between early sensitivity to face-like visual patterns and later development of face recognition itself, a development that may take advantage of an early emerging ability for aspecific (domain-general) visual expertise. It invites us to consider the difference between a sub-cortical route responsible for face detection and a cortical network of which the fusiform gyrus is a part, involved in face identification (Johnson, 2005b): in this case, the specialization for faces of the fusiform area is the product of its interactions with the sub-cortical route and the constant exposure to faces in the social environment. Competition, cooperation of brain components and chronotopy are jointly responsible

for the emergence of face recognition during development as a deeply entrenched cognitive feature. According to its proponents, this view is able to account for several phenomena: a) widespread brain activation in response to faces in young subjects (when specialization through competition has not yet occurred) that contrasts with specific local activation in elder subjects (Scherf and alii, 2007); b) the recruitment of the fusiform gyrus in tasks of visual recognition of non-face stimuli by experts in a given domain (Gauthier, Skudlarski, Gore, and Anderson, 2000); c) atypical developmental trajectories where defects of the sub-cortical processing of faces have cascading effects on other cognitive abilities and later phases of development (Johnson, 2005b). Neuroconstructivist explanations of this kind may be considered as a sub-type of what has been called by philosophers of science like Carl Hempel and Ernst Nagel *genetic explanations*. According to Hempel, a genetic explanation "presents the phenomenon under study as the final stage of a developmental sequence, and accordingly accounts for the phenomenon by describing the successive stages of that sequence" (Hempel, 1965, p. 447). This is still an appropriate description of the neuroconstructivist proposal, even if neuroconstructivist explanations do not fit Hempel's covering-law model of scientific explanation. "Mechanisms" like cooperation, competition and chronotopy are proposed to identify causally relevant factors (Craver, 2007) through their abstract, generic description, not merely regular sequences of events.

A view of brain development that is context-dependent in this sense may not only be accurate, but prove crucial for neuroethical issues. Some studies have shown a marked disadvantage for children of low economic status in tasks involving the prefrontal executive system, the left peri Sylvian language system, and the medial temporal memory system (Farah, Noble and Hurt, 2006). Potential causes range from prenatal substance exposure to nutritional factors (resulting in iron deficiency anemia), effects of environmental stress (the release of hormones that have a negative impact on hippocampal development, for instance) and lack of cognitive stimulation. Maturational views of neurocognitive development that suggest only a triggering role for environmental factors may seriously underestimate the impact of these factors not only on neurobiological, but also on cognitive development. Accordingly, neuroconstructivism may be important at two levels. First, from a theoretical point of view, it sides with an interactive view of individuation, where abilities supervene on the interactions of individuals and their environment during development. Neuroconstructivism may stimulate research on the nature and extent of such interactions. On a practical level, developmental neurobiology may give precious information on how, in matters of public health, we may become able to implement our norms of justice and fairness when it comes to child development.

## V

## Universal context-dependence? A critique

There is a close link, in the neuroconstructivist framework, between an *empirical* claim about neurobiological development and its central *theoretical* claim. The empirical claim concerns the relevant factors of an explanation of cortical development; it says that we should downplay the importance of genetic factors in such an explanation. In favor of that claim, neuroconstructivists offer two main reasons. The first is the role during development of epigenetic factors, in particular, activity-dependent mechanisms and adaptations like the ones that are crucial to the definition of ocular dominance columns (Mareschal and al., 2007, p. 21). The second is that true instances of region-specific gene expression in the cortex are not common: one notable case is the H-2Z1 transgene that is

expressed in only one region in mice, the layer IV of its somatosensory cortex (O'Leary and Nakagawa, 2002, p. 22). Accordingly, neuroconstructivists hold that although genes are involved in an early definition of broad regional differences, later specification of well-defined areas is mostly the product of activity-dependent processes (Mareschal and alii, 2007, p. 22). This empirical claim is offered as evidence by neuroconstructivists for the validity and heuristic value of the core principles of their model: universal context-dependence, interactive specialization of brain components governed by competition and cooperation.

"Context-dependence" is often understood in terms of dependence on interactions with the environment, internal but also external. One risk here is overgeneralization: from an evolutionary perspective, while it is obvious that both the level and the type of related activity may be crucial when it comes to the size or the function of a given area (Hunt, Yamoah and Krubitzer, 2006), it is hardly obvious that the global cortical architecture can be understood in terms of context-dependence. Comparison between species shows that the global organization of the mammalian cortex (its "Bauplan") is fairly conservative, differences in behavior notwithstanding (Krubitzer, 2007). For instance, sensory cortical fields are not context-dependent to the point that blind species like mole rats would be entirely deprived of visual structures: the architectural pattern remains strictly constrained and, to a large extent, context-independent. To take another example, recent work devoted to ocular dominance columns in primary visual cortex (Crowley and Katz, 2002) suggests that their emergence predates the first months of life, and as a consequence, cannot be the result of activity-dependent competition between thalamic inputs resulting from retinal stimulation. Although the formation of such columns may not be entirely independent from activity, as recent work on the role of retinal waves has shown (Torborg and Feller, 2005), what is crucial in this case is endogenous activity triggered by internal factors rather than actual visual experience.

Concerning epigenetic factors in general and activity-dependent change, some similar lessons could be drawn from the phenomenon of axon guidance. Constructivism since the days of Elman and his co-workers[10] have argued that we have to make a distinction between additive and substractive events, initial proliferation of synaptic connections during development and a later phase of "pruning" that corresponds to the degeneration of non-functional paths. This is conform to what is predicted by the epigenetic, "specialization through competition" model. But neural pathways do not develop in a purely anarchic manner before a negative phase of selective apoptosis and degeneration driven by competition. In particular, projection from thalamic regions to the isocortex may largely depend on patterns of regional expression of molecules that function as guidance cues (both positive and negative) for neurite outgrowth. For instance, expression of ligand Ephrin-2A5 in the somatosensory cortex inhibits projection from limbic thalamic afferents (Gao and alii, 1998). As expression of these molecules happens early in development, and *precedes* the invasion of the cortex by thalamic axons, it may be viewed as a context-*independent* factor of regional differentiation. This involves something that is very different from the predictions of the proliferation-and-pruning-model. The risk, then, is to neglect explanatory factors that do not fit the model, such as the ones suggested by the pioneering work of Sperry (Sperry, 1943) and his idea of chemo-affinity as a factor of organization during development. To sum up, from genuine instances of activity-dependence and thalamic influence we cannot conclude to their explanatory relevance in any given context. And although neuro-constructivists are right to distinguish between activity-dependence and (external) context-dependence (Mareschal et alii, 2007, p. 32), not only does spontaneous endogenous activity have a role where sensory experience has none for the establishment of visual circuity, but it seems that we also have to take into account activity independent factors (Huberman, Feller and Chapman, 2008).

[10] Elman, 1996, p. 245.

Concerning the second empirical claim, the one concerned directly with genes, even if it remains true that there is no one-to-one correspondence between genes and cortical areas, and even if knowledge in these matters is still fragmentary, and based mainly on studies that focus on a single species (mice), not only has evidence of genetic control of arealization been growing in the last twelve years, but this may be considered as the main recent event in the field of the neurobiology of cortical development (O' Leary and Sahara, 2008). For instance, gene Emx2 is normally expressed in low rostral to high caudal and low lateral to high medial gradients, and cadherin Cad 8 is a special attribute of motor cortex situated in the rostrally located motor cotex. In Emx2 homozygous mutant mice, however, it has been discovered that the pattern of cadherin expression is markedly altered, expression of Cad8 being expanded both caudally and medially while caudal areas contract. Moreover, in Emx2 mutant mice, connections between cortical areas and thalamic nuclei are significantly altered, arguably because of the involvement of Emx2 in the differential production of molecules controlling axon guidance: while in wild-type mice, the anterior occipital cortex receives projections from the dorsal lateral geniculate nucleus, which conveys visual inputs, in mutant mice, the same region receives projections from the ventroposterior nucleus, which are normally characteristic of the somatosensory cortex, a clear sign of the contraction of the visual area (Bishop, Goudreau and O'Leary, 2000). Accordingly, as molecular expression and patterns of connectivity are two of the most important attributes of cortical areas, we may conclude that genetic control, in some species at least, goes much further than the rough preliminary definition of whole regions whose internal architecture would be fine-tuned under the influence of epigenetic factors. Moreover, the choice is not between a one to one correspondence between genes and cortical areas and no genetic mediation of cortical development whatsoever: genes like Emx2, Pax6 and COUP-TFI are expressed in the cortex according to gradients that may overlap in such a manner that taken together, they play a crucial role in the definition of the emergence of the combination of features that is unique for each area (Kingsbury and Finlay, 2001).

However suspicious we may be, then, of the metaphor of traits being directly coded or represented in sequences of DNA basis, we do not have to conclude from the fallacy of outdated genetic determinism to the validity of rival constructivist proposals when it comes to the explanation of cortical development. Explanations of arealization now begin with patterning centers contained in the dorsal telencephalon of the developing brain (O' Leary and Sahara, 2008). These patterning centers secrete a series of molecules (like the fibroblast growth factor FGF8) which are in turn, responsible for the differential expression of genes like Emx2, Pax6 and COUP-TFI in progenitor cells and their progeny in cortical regions. This proposal deserves several comments. First, it could be said with reason that expression of genes in this model is context-dependent; but this kind of dependence has to be understood in the perspective of a "regulatory hierarchy" (O' Leary and Sahara, 2008) that secures the emergence of a quite uniform and highly adaptive cortical structure. It is not "horizontal" interaction between equals (genes, cells), but hierarchical control that seems to matter the most. Second, even if constructivists are right to insist on the importance of the timing of events during development ("chronotopy") it seems difficult to understand what this timing depends on without reference to the above-mentioned regulatory hierarchy, and for instance, to early secretion of signaling molecules on which gene expression is dependent. Third, in agreement with an influential view of mechanistic explanation (Machamer, Darden and Craver, 2000), explanation of cortical development is not achieved by pointing exclusively to low-level, "bottoming-out" components of cortical structures, but through the careful description of the integration of entities and activities located at different levels of the mechanism. We have to adapt this model in a developmental context: "mechanism" does not refer here to a static set of components, but to a self-modifying structure where interactions are responsible for the addition of new features and operations. But the lesson remains: explanation of phenomena at higher levels of mechanism is neither reducible to bottoming-out entities and activities, nor divorced

from them. To sum up, even if the shift from gradients of gene expression to the abrupt contrast between discrete cortical areas is not fully understood, it seems that there is no mechanistic explanation of cortical development without a reference to this regulatory hierarchy of which gene expression is a key part, a proposition that is not easy to reconcile with the spirit of the neuroconstructivist program which favors "horizontal" interactions and epigenetic factors.

The neuroconstructivist program aims to make explicit "lessons" from past studies that "should help us to identify the relevant questions, factors and variables that will lead us to a deeper understanding of development" (2007, p. 91). It does not seem that its "principles" are to be understood as statements of universal laws of nature; it is nowhere said, for instance, that *comparative* developmental neurobiology would support claims of necessity or universality in these matters. What is offered by neuroconstructivists seems rather to be heuristic principles that may function as guidelines for future research. However, neuroconstructivist principles may suffer, first, from overgeneralization : it may be that what is valid and heuristically useful for late stages of development and mid-level organization may not have the same value for earlier phases and/or lower levels of organization (see Kingsbury and Finlay, 2001, and their distinction between "early cortical regionalization" and "late cortical regionalization"). Second, these same principles may suffer from under-specification, as was already noticed, not only because specialization may be understood in more ways than one (Anderson, 2008) but because of the wide differences between types of context-sensitivity. Unless we define unambiguously a) which degrees of change are significant enough to be counted as evidence of sensitivity (that is, as a mark of dependence), b) what is evidence of causal dependence to context, and above all c) what is exactly the context (with its specific boundaries and properties) a given event is supposed to depend on in a given case; it will be very difficult to establish what exactly confirms or disconfirms the principle of context-dependence. Moreover, the kind of interactions between components we have to understand is not always the one that is predicted by neuroconstructivism: often, context-dependence involves hierarchical control within a multi-level developmental mechanism, rather than cross-talk among equals at a given level.

## VI Conclusion

Very often, constructivism is perceived and debated as an alternative to nativism, as if arguments and empirical predictions could lead to a final settlement of the dispute. It is reasonable to think, however, that scientific investigation itself is inherently pluralistic, that developmental neuroscience, as understood by neuroconstructivists, evolutionary neuroscience, and "systemic" neuroscience, ask, to use van Fraasen's terminology, different "why-questions", the topic of each of them being associated with a different "contrast class" (van Fraassen, 1980). One of the main interests of the developmental perspective is that atypical development is not necessarily synonymous with dysfunction, impairment and cognitive failure, as was shown by recent work on high-level autism (Happé, 1999). But the classical framework of neuropsychology, with its contrast between brain or cognitive integrity and deficits associated with lesions, if not relevant to the field of developmental syndromes, is still valid in its proper context. Neuroconstructivism may (and does) inspire quite promising research (Rippon, Brock, Brown, and Boucher, 2007) with valuable theoretical and social implications, but different perspectives are still needed. Pluralism, as it is advocated here, does not preclude cross talk between existing disciplines, and the birth of new integrating disciplines at their borders (evolutionary developmental neuroscience would be an example). But it precludes seeing a proposal like neuroconstructivism and the new emphasis on development in terms of "developmental turn" or paradigm shift.

Philosophers interested in neuroconstructivism may face the following alternative. One possibility is to use the neuroconstructivist framework to build a broad view of development and human nature. The other possibility is to reflect on the program itself and its current limitations. The second possibility defines one possible task for the philosophy of neuroscience. On the one hand, if mechanisms have been the focus of attention in recent years in the field of philosophy of neuroscience, the developmental perspective is an occasion to consider these mechanisms in a different light: mechanisms and their characteristic activities are not only the producers of change, they are also the products of change, something we need to understand if we want to know how they become capable of doing what they do. On the other hand, the core idea that mechanisms typically span multiple levels (Machamer, Darden and Craver, 2000; Craver, 2007) is still fruitful in this different context, as it cures us both from strict fundamentalism (only lower levels matter) and vague emergentism. In particular, it is only in defining the role of genes in the containing systems where they are embedded, and it is only in considering the phenomenon of arealization in its relation with its tight but complex genetic control, that developmental neuroscience will be able to overcome the present limitations of the rhetoric of "construction".

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