

Neuroconstructivism

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Abstract

Neuroconstructivism is a theoretical framework focusing on the construction of representations in the developing brain. Cognitive development is explained as emerging from the experience-dependent development of neural structures supporting mental representations. Neural development occurs in the context of multiple interacting constraints acting on different levels, from the individual cell to the external environment of the developing child. Cognitive development can thus be understood as a trajectory originating from the constraints on the underlying neural structures. This perspective offers an integrated view of normal and abnormal development as well as of development and adult processing, and it stands apart from traditional cognitive approaches in taking seriously the constraints on cognition inherent to the substrate that delivers it.

Introduction

One of the greatest challenges in developmental psychology is to explain the mechanisms of cognitive change. However, much of developmental psychology is concerned with exploring children's abilities at specific ages without devoting equal attention to the question of the mechanisms by which these abilities unfold and change over time (Shultz & Mareschal, 1997). Explaining cognitive change requires a theory that can link the observed abilities of infants and children at different ages into one developmental trajectory. Such a theoretical framework is presented in a recent book, *Neuroconstructivism* (Mareschal, Johnson, Sirois, Spratling, Thomas & Westermann, 2007; see also Karmiloff-Smith, 1998).

A central tenet of the neuroconstructivist approach is a focus on the factors that influence the emergence of mental representations in postnatal development. Representations are here defined as neural activation patterns in the brain that contribute to adaptive behaviour in the environment. Therefore, understanding cognitive development requires an understanding of how the neural substrates supporting mental representations are shaped. Neuroconstructivism views the development of these neural systems as heavily constrained by multiple interacting factors intrinsic and extrinsic to the developing organism. From this perspective, the cognitive developmental

trajectory occurs in the context of the constraints operating on the development of the brain. These constraints span multiple levels of analysis, from genes and the individual cell to the physical and social environment of the developing child. However, as we shall see, it is possible to identify common principles that operate across all these levels.

Although this approach to cognitive development might seem to advocate reductionism by attempting to explain cognitive change on the neural level, such an interpretation would be misleading. Neural development, especially in the cerebral cortex, is often dependent on neural activity which can be mediated by experience with the environment. Therefore, cognitive processing itself shapes the neural networks that are responsible for this processing in the first place. These changes to the brain's 'hardware' in turn change the nature of representations and their processing, which leads to new experiences and further changes to the neural systems. Therefore, the basis of cognitive development can be characterized by mutually induced changes between the neural and cognitive levels. Importantly, this view implies a rejection of independent levels of description that are often advocated in cognitive psychology (Marr, 1982). Because algorithm and hardware change each other in development, they cannot be studied in isolation. Instead of independent levels of analysis or neural reductionism, neuroconstructivism calls

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for *consistency* between the neural and cognitive levels in characterizing developmental trajectories.

The neuroconstructivist approach has been motivated by advances in developmental research that enable the investigation of cognitive and brain development in parallel. First, in the past ten years our ability to investigate the developing brain has progressed dramatically through the advent of sophisticated imaging methods such as ERP, MEG, fMRI and NIRS (e.g. Casey & de Haan, 2002). Second, at the same time new paradigms have been developed to examine the abilities of even very young infants in a variety of behavioural domains (Aslin & Fiser, 2005). And third, computational and robotic models have become established as a methodology to develop and test specific hypotheses of the interactions between brain and cognitive development (Asada, MacDorman, Ishiguro & Kuniyoshi, 2001; Elman, 2005; Lungarella, Metta, Pfeifer & Sandini, 2003; Mareschal, Sirois, Westermann & Johnson, 2007; Westermann, Sirois, Shultz & Mareschal, 2006).

Constraints on development

In the neuroconstructivist framework, understanding the constraints on neural development is a central aspect of understanding cognitive development. By taking into account constraints on all levels from the gene to the environment, neuroconstructivism integrates different views of brain and cognitive development such as (1) probabilistic epigenesis which emphasizes the interactions between experience and gene expression (Gottlieb, 1992), (2) neural constructivism which focuses on the experience-dependent elaboration of small-scale neural structures (Quartz, 1999; Quartz & Sejnowski, 1997), (3) the 'interactive specialization' view of brain development which stresses the role of interactions between different brain regions in functional brain development (Johnson, 2000), (4) embodiment views that highlight the role of the body in cognitive development (e.g. Clark, 1999), (5) the constructivist approach to cognitive development (Piaget, 1955) with its focus on the pro-active acquisition of knowledge, and (6) approaches focusing on the role of the social environment for the developing child.

Genes

The traditional view of gene function holds that there is a one-directional flow of cause and effect from genes (DNA) to RNA to the structure of proteins they encode. From this perspective, development consists in the progressive unfolding of information that is laid out in the genome. However, more recent research presents a subtler

picture by showing that environmental and behavioural influences play a fundamental role in triggering the expression of genes (reviewed e.g. in Lickliter & Honeycutt, 2003). This *probabilistic epigenesis* view of development (Gottlieb, 1992) emphasizes that gene activity, instead of following a strictly pre-programmed schedule, is regulated by signals from the external and internal environment and that development is therefore subject to bidirectional interactions between gene activity, neural activity, behaviour and the environment. For example, in canaries and zebra finches the expression of ZENK, a gene involved in regulating synaptic plasticity and learning, has been found to be closely related to experience. The motor activity involved in singing has been shown to lead to a rapid increase of expression of this gene in motor areas, whereas hearing song induced expression of the same gene in parts of auditory areas (Jarvis, Xiong, Plant, Churchill, Lu, MacVicar & MacDonald, 1997). Furthermore, the amount of expression varied with the specific songs that were experienced: it was greatest when birds heard songs of their own species and lower for songs from other species (Mello, Vicario & Clayton, 1992). These results show that gene expression can be influenced in very specific ways by experience with the environment.

Encellment

The development of a neuron is constrained by its cellular environment throughout development. Even at the earliest stages of fetal development, the way in which a particular cell develops is influenced by molecular interactions with its neighbouring cells (Jessell & Sanes, 2000). At later stages of development, neural activity, either spontaneously generated or derived from sensory experience, begins to play an important part in the formation of neural networks (for a recent overview see Shultz, Mysore & Quartz, 2007). Neural activity is responsible both for the progressive elaboration of neural connection patterns as well as their subsequent stabilization and loss (neural constructivism; Quartz & Sejnowski, 1997). The remodelling of axonal and dendritic branches can occur rapidly with parallel progressive and regressive events (Hua & Smith, 2004). A higher rate of structural elaboration compared with retraction leads to a gradual overall increase in network complexity.

The specific role of neural activity in the formation of neural networks has been extensively studied in the development of ocular dominance columns (ODC). ODC are areas of primary visual cortex (arranged in stripes or patches) where neurons selectively respond to inputs from only one eye. The initial formation of these columns is likely to be dependent on pre- and postnatal spontaneously

generated neural activity (Feller & Scanziani, 2005). During a subsequent critical period, altered visual experience can lead to changes in ODC organization. For example, transiently closing one eye during early postnatal development results in shrinking of the columns responding to the closed eye and expansion of the columns responding to the open eye (Antonini & Stryker, 1993; Hubel & Wiesel, 1963). These results suggest that activity-based competition between neurons for synaptic connections is a driving mechanism in the establishment of precise connection patterns (Stryker & Strickland, 1984). Initially the same cortical area is innervated by axons from both eyes (via the thalamus) and activity-based competition leads to retraction of axons from one eye and elaboration of axonal branching for neurons from the other eye in each area (Katz & Shatz, 1996).

From a neuroconstructivist perspective these findings are important because they show how experiences can alter the neural networks that support the processing of these experiences. Neural activation patterns that form representations in the neuroconstructivist sense are constrained by the morphology and connection patterns of their underlying neural structures. However, the activation patterns themselves lead to morphological change, thereby altering the constraints imposed on representations. In this way, progressively more complex representations can be built by adapting the constraints (neural structures) to the experience (neural activation patterns) of the individual (Figure 1).

Embrainment

As the brain is embedded in a body (embodiment), so an individual functional brain region is embedded in a brain where it co-develops with other brain regions

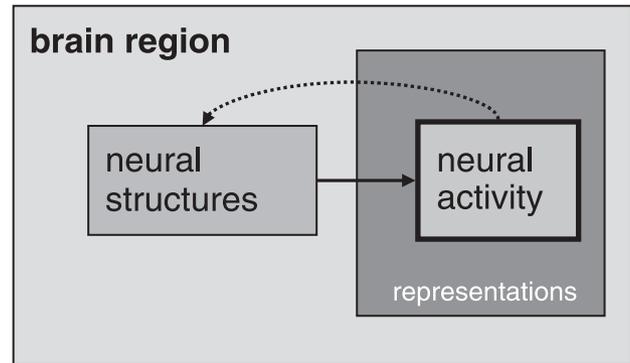


Figure 1 *Emcellment.* Neural activation patterns (corresponding to representations in the neuroconstructivist sense) are constrained by their underlying neural structures, but in turn effect changes in these structures through experience-dependent processes. (The solid line indicates a constraining relationship and the dashed line indicates the induction of change.)

(Figure 2). This embrainment view (Johnson, 2005) contrasts with a modular perspective which focuses on the development and functioning of specialized brain areas in isolation. It is supported by neuroimaging studies suggesting that the functional properties of a brain region are strongly context sensitive and constrained by its interactions with other regions, for example through feedback processes and top-down interactions (Friston & Price, 2001). Examples for the importance of inter-regional interactions in brain development can be found in studies with people who lack one sensory modality. For example, in people blind from an early age, the cortical area activated by Braille reading corresponds to the primary visual cortex in sighted people (Sadato, Pascual-Leone, Grafman, Ibañez, Deiber, Dold & Hallett, 1996). Apparently therefore, brain regions that normally

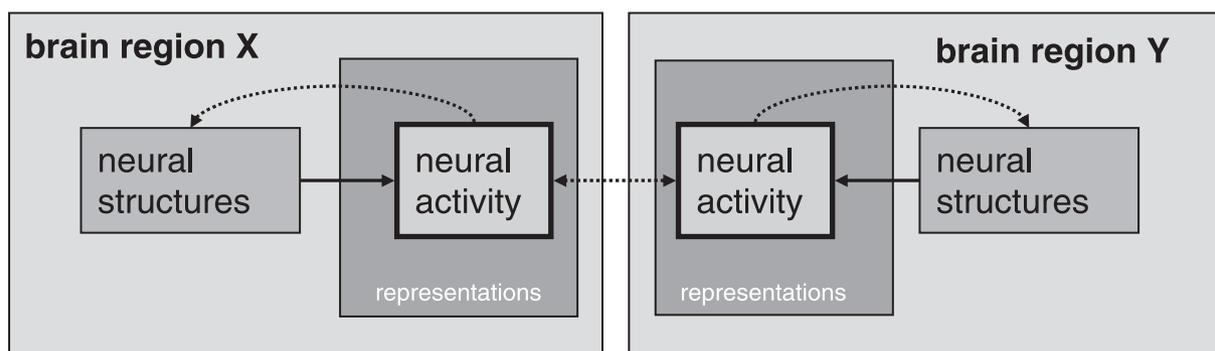


Figure 2 *Embrainment.* Two functional brain regions develop interactively. While each region is shaped by experience-dependent mechanisms, inter-regional interactions can alter the activity pattern within a region and thus the underlying neural structures in this region. In this way, one developing brain region can contribute to the nature of developing representations in another region. (Solid lines indicate a constraining relationship and dashed lines indicate the induction of change.)

process visual information can take on a different functional role in the absence of visual input. That this new role is functionally relevant was shown by transiently disrupting processing through transcranial magnetic stimulation (TMS) (Cohen, Celnik, Pascual-Leone, Corwell, Falz, Dambrosia, Honda, Sadato, Gerloff, Catala & Hallett, 1997). It turned out that TMS stimulation of the visual cortex disrupted the tactile identification of Braille letters in the blind but not in sighted participants. Instead, sighted participants displayed disrupted visual performance after TMS stimulation of primary visual cortex (Amassian, Cracco, Maccabee, Cracco, Rudell & Eberle, 1989). Therefore, the adaptive development of the functional organization of cortical areas seems to depend strongly on the available sensory inputs, with the final organization emerging through interactive processes such as competition for cortical space (Johnson, 2000). This *interactive specialization* view implies that cortical regions might initially be non-specific in their response but gradually sharpen their responses as their functional specialization restricts them to a narrower set of circumstances. Such a gradual sharpening of activated cortical regions for a specific process has for example been identified in word learning (Mills, Coffey-Corina & Neville, 1997) and face processing (Passarotti, Paul, Russiere, Buxton, Wong & Stiles, 2003).

The interactive specialization view can be extended to account for the developmental integration of different (often cortical and subcortical) brain regions for a specific ability. An integration of different brain areas has been used to explain behavioural change in the development of face recognition (Morton & Johnson, 1991), object-oriented behaviour (Mareschal & Johnson, 2003), memory (Munakata, 2004), categorization (Mareschal & Westermann, in preparation), habituation (Sirois & Mareschal, 2004), speech (Guenther, Ghosh & Tourville, 2006; Westermann & Miranda, 2004) and language (Mills *et al.*, 1997).

Embodiment

The mind exists within a body that is itself embedded in a physical and social environment. This fact both constrains and enhances the experiences of a developing child. Neural activation patterns are generated by sensory inputs, and therefore the functioning of the sensory organs has a highly constraining effect on the construction of representations in the mind. In this sense the body acts as a filter for information from the environment. Two examples for this body-as-filter aspect of embodiment are the limited visual acuity and the limited motor control of the young infant which restrict the infant's possible sensory experiences and thus limit the potential

complexity of representations at this developmental stage. It has been argued that the gradual loosening of physical restrictions might be beneficial to allow for an orderly developmental trajectory with a gradual increase in the perceived complexity of the environment and resulting progressively complex representations (Turkewitz & Kenny, 1982).

However, the developing body not only serves as a filter for information, but also as a means to manipulate the environment and to generate new sensory inputs and experiences. For example, even newborn infants will intentionally move their arm into a light beam, resulting in an illuminated spot on the limb that is not visible unless the limb is moved to the correct location (van der Meer & van der Weel, 1995). The reward for seeing the light spot completes a feedback loop between the infant and her environment, changing this environment to generate specific sensory inputs. At later ages infants use their increased mobility and sensorimotor coordination to explore and manipulate their environment further, generating ever more sensory inputs which in turn lead to the modification of neural networks and to the construction of more complex representations (Figure 3).

The embodiment view emphasizes that pro-activity in exploring the environment is a core aspect of cognitive development: the child does not passively absorb information, but through manipulating the environment selects the experiences from which to learn. It also shows that what can be called the 'classic' model of cognition – the mind acquiring rich representations of the external world, operating off-line on these representations, and generating an output – neglects the important aspect of real-time interactions with a changing world. An embodied alternative to the classic view emphasizes multiple real-time adjustments to the coupled brain–body–environment system to coordinate between inner and outer worlds (Kleim, Viji, Ballard & Greenough, 1997).

Ensocialment

The specific environment in which the developing child is situated has a highly constraining effect on the emergence of neural representations because it restricts the possible experiences of the child and offers to her certain ways in which it can be manipulated. These constraints refer mainly to the physical properties of the environment. Another source of constraints concerns the social aspects of the environment, for example the interactions between a caregiver and her child. It has long been recognized that synchronous interactions between mother and child have a strong effect on the development of a secure attachment, the expression of emotions, social and cognitive

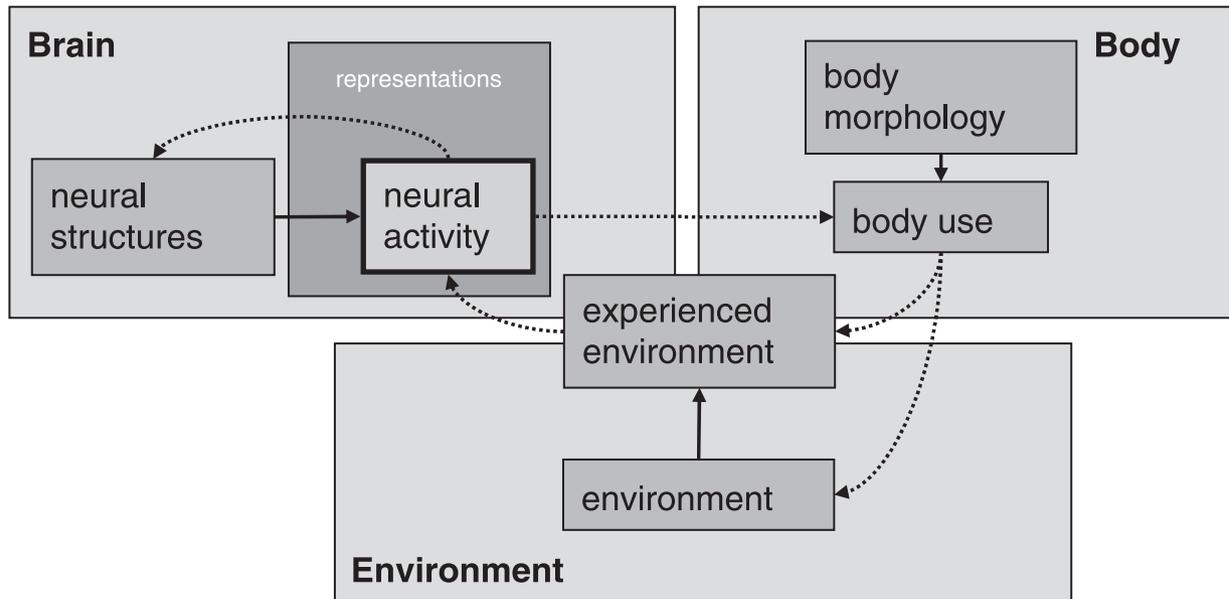


Figure 3 Embodiment. The brain is closely linked to its body and the environment. Body use, constrained by the body's morphology, can generate novel sensory experiences through altering the experienced environment. This can be achieved either by moving the sensory organs (e.g. the eyes) without changing the external environment, or by manipulating the environment itself. The experienced environment generates neural activity which, through encllement, leads to changes in the underlying (and, through embrainment, in other) brain systems. For simplicity, different brain regions are here collapsed into one. (Solid lines indicate a constraining relationship and dashed lines indicate the induction of change.)

development (reviewed in Harrist & Waugh, 2002). By contrast, disrupting a normal mother–infant relationship and exposure to early stressors such as death of a caregiver, child abuse or neglect, can have profound effects on the neural and behavioural development of the infant (Cirulli, Berry & Alleva, 2003; Kaufman, Plotsky, Nemeroff & Charney, 2000).

Interactions between constraints

The described constraints on neural development interact in different ways to shape the construction of representations in the brain (Figure 4). Neural development itself depends on experience-derived neural activity which can lead to changes in gene expression. Experience-dependent changes not only occur in the formation of within-region networks but also in between-region pathways. Interactions with a social environment have effects on both neural development and on the expression of genes (Eisenberg, 1995). These effects can either be mediated through direct experience with the environment or through altered caregiver behaviour in a specific environment (Sale, Putignano, Cancedda, Landi, Cirulli, Berardi & Maffei, 2004). Put together, in the development of cognitive processing, these constraints form an

interactive network shaping the neural structures that form the basis of mental representations.

The nature of representations

How can the multiple biological and environmental constraints that shape the neural system inform our understanding of the nature of mental representations? From the constraints on the development of neural structures we have derived a number of principles that characterize the emergence of representations (Mareschal *et al.*, 2007). The main principle is *context dependence*. On all levels of analysis the shaping of neural structures giving rise to mental representations is highly dependent on the context in which these structures develop. This is true for the cellular context of the individual neuron, for interactions between brain regions, and for the physical and social environmental context of the child. Like their underlying neural structures, mental representations are shaped by processes involving *competition* and *cooperation*. Competition ensures that the developing components of a system become specialized on different aspects of processing, driving the system towards representing new information. By contrast, cooperation leads to the integration

the construction of neural networks allows for a unified view of normal and abnormal development as well as development and adult processing. Developmental disorders can be understood through altered constraints that push the developmental trajectory off its normal track to reach a different endstate (Karmiloff-Smith, 1998; Thomas & Karmiloff-Smith, 2002). Thus, atypical development can, like typical development, be characterized as an adaptation to multiple interacting constraints, only that the constraints are different. These atypical constraints then lead to different outcomes through the same processes of representation construction. This explanation of atypical development stands in contrast to theories which assume that disorders arise from isolated failures of particular functional modules, for example the failure of an innate dedicated 'theory of mind module' in autism (Frith, Morton & Leslie, 1991) or selective damage to a genetically pre-specified syntactic module in Specific Language Impairment (van der Lely, 2005). Instead, due to the context-dependent nature of development, atypicalities in one part of the system are likely to have ramifications in other parts within the system and in interactions with the environment, leading to a final state that is optimally adapted to the specific set of constraints (Thomas & Richardson, 2006).

The neuroconstructivist framework also provides an integrated view of development and adult processing because the adult state is viewed as merely a (more stable) state along the developmental trajectory. From this perspective the investigation of adult processing benefits from being analyzed through a developmental lens to reveal which constraints have shaped development to reach the adult state. Adult cognitive processing is often characterized as consisting in a set of qualitatively different, specialized, domain-specific modules. The neuroconstructivist perspective instead focuses on how regions of functional specialization are formed given the outlined constraints, providing explanations of adult processing that are less focused on qualitatively different encapsulated modules.

Neural network and robotic modelling offers an excellent tool for understanding development from a neuroconstructivist perspective (Mareschal, Sirois *et al.*, 2007; Thomas & Karmiloff-Smith, 2003; Westermann *et al.*, 2006). This is because in models different constraints (such as network structure, mechanisms of neural information processing and experience-dependent structural change, environmental complexity and the ability to interact with the environment) can be systematically varied and the effect of this variation on performance can be investigated in detail. These models therefore offer the opportunity to explore the link between multiple interacting biological and environmental constraints,

neural development, and the development of cognitive representations.

Conclusions

Neuroconstructivism offers a theoretical framework in which cognitive development is closely linked to the development of the underlying neural structures in the brain. By characterizing the constraints that operate on the development of neural structures that support mental representations, cognitive development is explained as a trajectory emerging from the interplay of these constraints. This view provides a unified framework for analyzing normal and abnormal development and it offers a view of adult processing as an outcome of development. Importantly and in contrast to other approaches to psychological research, neuroconstructivism implies that the widely accepted independence of levels of description defended by Marr (1982) does not hold. Instead, consistency between levels is necessary because of interactions across levels: computations on Marr's computational level have direct effects on the hardware level which changes the processing algorithm through progressive representation construction, leading to new computations with further effects on the hardware.

Progress in research in the neuroconstructivist framework will be made by a better understanding of the constraints operating on neural development, by improved methods of linking brain and behaviour in developing children (see also Aslin & Fiser, 2005), and by computational modelling which has the potential to offer explanations of the interactions between brain and cognitive development (Mareschal, Sirois *et al.*, 2007; Westermann *et al.*, 2006).

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