Chapter 15

New Developments in Neuroconstructivism

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New Developments in Neuroconstructivism

*"*Nature abhors a vacuum*", Aristotle*

Aristotle's words are generally understood to mean that the absence of something is quickly filled by another substance throughout the natural world. But it also means that nothing exists in isolation! All natural systems are embedded within and interact with the systems that surround them. This is a fundamental truth of development; a child does not grow up in a vacuum. The primary aim of this volume is to explore the development of, and *interactions* amongst, three information-gathering components that are critical to early development: attention, learning, and memory. To this end, the current chapter explores a highly influential framework that can be used to understand how these interactions can occur and how they can shape together the development of social, perceptual and cognitive abilities.

Neuroconstructivism (Mareschal et al., 2007a, 2007b; Westermann et al., 2007) is a theoretical framework for understanding brain and cognitive development. According to this theory, the developmental trajectory of brain networks that give rise to progressively more complex mental representations occurs within the context of multiple interacting biological and environmental constraints across development. *Neuro*constructivism is an adjunct of *Neo*constructivsm. According to constructivist theories, cognitive development is a continual process of building and restructuring knowledge on top of the foundations laid down by existing knowledge. Neoconstructivist theories have attempted to update Piaget's constructivist ideas (e.g., Piaget, 1970) by situating them in the context of a more modern understanding of child cognitive development. *Neuro*constructivism is a theory situated squarely within this more contemporary approach to constructivism; it focusses more on the brain and considers it to be self-structuring and dynamically changing over developmental time, and with a foundational principle of *context dependence*. Neuroconstructivism argues that the same family of developmental constraints operate across all levels of representation… from cellular environments, to brain neural networks, and to the social and physical environments in which the organism develops. In viewing the brain as dependent on its current and previous environment, Neuroconstructivism provides an account of how the continuous interactions that exist between the organism and the local constraints that operate at different levels of description gradually give rise to the specialised adult brain and adult cognitive abilities.

Since its appearance in the literature some 18 years ago, the Neuroconstructivist framework continues to influence how contemporary researchers formulate their questions and interpret their empirical findings in the context of the development of attention, memory and learning (e.g., Oakes, 2023; Wass, 2021; Bettoni et al, 2024), as well as shaping theories of developmental conditions (e.g., Johnson, 2021;

Perry et al., 2024; Astle et al., 2024) and sociocultural development (Benardo, 2024). For those familiar with Neuroconstructivism – that it is a rapprochement of Neoconstructivist theories of cognitive development and theories of functional brain development, that it posits constraints acting on development including *encellment*, *embrainment*, *embodiment* and *ensocialment*, that it posits mechanisms that include *cooperation*, *competition* and *chronotopy*, and processes of *proactivity* and *progressive specialisation*, which together lead to the developmental outcome of partial representations – if these are familiar concepts, then you should skip ahead to Section 2 to see what's new. For those not familiar with Neuroconstructivism, the following section introduces these ideas and shows their relevance to attention, learning, and memory.

In the rest of this chapter, we first describe the initial 2007 Neuroconstructivist framework in more detail, focussing on the mechanisms and processes of change at the heart of this framework. We then turn to one specific element, *Interactive Specialisation*, and ask how empirical work over the last 18 years has attempted to test and validate (or refute) this manifestation of the Neuroconstructivist approach. Finally, in a third section we explore how Neuroconstructivism can be extended to the genetic level of description and how evolution can be incorporated within this framework, along with the shift in focus that these extensions entail.

The origins of Neuroconstructivism

In *Neuroconstructivism: How the Brain Constructs Cognition* (Mareschal et al., 2007), different approaches to human development such as cognitive neuroscience, computational modelling, constructivism, and probabilistic epigenesis are integrated into a single coherent framework. This has allowed for the examination of constraints that operate on development at all levels of representation, from cells to the social environment. As will be discussed in more detail below, Neuroconstructivism provided a response to traditional nativist and empiricist stances on cognitive development (Karmiloff-Smith, 2009). The emergence of Neuroconstructivism was in part supported by advances in neuroscientific methods for investigating the developing brain. These include (but are not limited to) non-invasive brain imaging techniques such as event-related potential (ERP), functional magnetic resonance imaging (fMRI), magnoencephalography (MEG) and near infra-red spectroscopy (NIRS). Studies of early infant development that have employed these techniques have highlighted how the brain and cognition co-develop within a dynamic environment (Johnson, 2000). In addition, computer and robotic simulations are now also frequently employed to help understand the close link that exists between cognition and the brain (e.g., Westermann et al., 2006; Mareschal & Thomas, 2007; and more recently Astle, et al., 2023). Models go beyond limited descriptive theories by allowing researchers to test the plausibility of different proposed mechanistic theories of cognition. Artificial neural network models are computer models that try to mimic some aspects of what is known about information processing in the brain. They can therefore be used to test ideas we have about how learning and development can co-occur in the child's developing brain. Finally, advances in understanding epigenetics have also highlighted the fundamental role of behavioural and environmental influences on gene expression (Gottlieb, 2007). Importantly, gene expression is now considered to be a contextual and bidirectional influence on development. It is not equivalent to an inevitable "come-what-may" decryption of a prespecified program or set of static and immutable instructions that are somehow encoded in the genome.

Through the integration of these different approaches and methodologies, the Neuroconstructivist framework provides a middle ground between a domain-specific nativist approach and a domain-general empiricist view of brain development. In the first instance, Neuroconstructivism stands in contrast to a modular, nativist stance on cognitive development, which advocates for genetic determinism, the hard-wiring of brain states, and innate specification of dissociated modules in the human brain that operate in isolation. Instead, Neuroconstructivism considers cognitive functioning as an emergent property, inextricably linked to the underlying neural substrates, and which is mediated by the dynamic environments in which the organism operates. According to this view, cognitive functions are not considered to operate in isolation, but within the context of many interacting factors and constraints at multiple levels of analysis. These contextual factors consist of aspects both intrinsic (e.g., neural, chemical, physiological) and extrinsic (e.g., social and physical environments) to the developing organism.

In the second instance, the Neuroconstructivist approach stands in contrast to empiricist views of the brain as a 'blank slate' in which any cortical region can equally support any input or process. In contrast, Neuroconstructivism recognises that small regional differences in the neonate cortex in neuronal type, orientation and firing thresholds, synaptic density, balance of neurotransmitters, and neuronal formation and so forth, are neither domain-specific nor domain-general. Rather, small regional differences that could be considered 'domain-relevant' processing, are thought to become more akin to 'domain-specific' and even 'modular' outcomes over developmental time with repeated processing of certain types of input and the gradual settling of competition with other brain regions. This fundamentally shifts debates about "innateness" away from discussion of representational innateness (in which knowledge is somehow encoded or hardwired in the brain independently of experience) to a discussion of what learning biases are in place that will drive certain functional systems to specialise in one or another domain as a result of environmental experience, often generated by the organism's own behaviour (cf. Elman et al., 1996).

The constraints operating on development

A central tenet of Neuroconstructivism is ***context-dependence***. This refers to the constraints that operate on development at different levels of analysis and *how* these constraints impact on the development of the brain neural networks that underpin cognition. The foundational principles of Neuroconstructivism include the contextual effects of *encellment*, *embrainment*, *embodiment*, and *ensocialment*, each of which are clarified in turn below.

Encellment: Encellment denotes the concept that the functions a neuron will ultimately take on in the brain are dependent on its cellular and chemical environment throughout development. From the very earliest point in brain development, the elaboration and stabilisation of functional neural networks is influenced by the surrounding environment and by cell-to-cell interactions. Ultimately, the function and structure of the cells themselves is determined by the chemical environment that they find themselves in early in brain development, the function of the neighbouring cells, and development of connections between these cells in response to experience with the external environment. In this sense, even at the cellular level, brain development is fundamentally about embedding consistently with a local environment.

Embrainment: By the same premise that bidirectional interactions are at play at the cellular level, Neuroconstructivism also takes into consideration that functional areas of the brain are embedded and operate within a context of connections to and from other functional regions of the brain (see also Johnson's 2001, concept of *Interactive Specialisation*). In this way, not only are brain regions presumed to mature within the context of other regional changes, but also cognitive functions associated with specific brain regions in the adult end-state are highly constrained by current and past interactions with other brain areas. Support for interregional interactions in brain development comes from studies with individuals who lack one sensory modality. For example, cortical regions that are activated during braille reading in congenitally blind subjects correspond to areas in the primary visual cortex in sighted individuals (Sadato, Pascual-Leone, Grafman, & Ibañez, 1996). The nature of mental representations generated through neural activation patterns is constrained not just by the structure of the neural networks supporting these patterns, but also very much by the nature and structure of the neighbouring neural networks.

Embodiment: The existence of the mind within a body is seen to serve both to enhance and constrain the experiences of the developing child. The embodiment view of Neuroconstructivism highlights the importance of an organism's active exploration and manipulation of their environment, by which new sensory inputs and experiences are generated at different points across development. Limited visual acuity and motor control during infancy are cited as examples of bodily constraints that restrict an infant's potential sensory experiences and complexity of subsequent mental representations at this stage of development. However, the gradual easing of these restrictions with increased mobility and sensorimotor coordination serves to increase perceived complexity of the environment, and is considered to be beneficial for the developing infant by facilitating perceptual organisation in a protracted fashion (Turkewitz & Kenny, 1982). The individual is not seen as a passive agent soaking in experiences. Instead, by manipulating their own environment the individual selects the experiences from which to learn, again highlighting the bi-directional impact of constraints at different levels. Finally, as a species, we have invented external tools such as writing and calculators that greatly help extend our cognitive abilities by situating them within an external world (see Clark, 1997).

***Ensocialment**:* In Neuroconstructivism, the emergence of mental representations is inextricably related to the specific physical and social environment in which the child develops. By restricting the possible experiences a child will have, the physical properties of a child's environment are understood to have a constraining effect on the extent to which a child can develop mental representations of environmental stimuli. Similarly, the social environment has profound effects on the neural and behavioural development of an individual, particularly during early development (e.g., Champagne & Curley, 2005). In Neuroconstructivism, the contextual effect of ensocialment is seen across different levels of description. For instance, constraints are considered to operate from the level of early precursors to social interactions (e.g., face and gaze processing), emergence of a 'social brain' network of regions during childhood, the cultural impact of language on the development of mental representations, to the role of parent-child/ teacher-child interactions on cognitive development. For example, Barbara Rogoff (2003) describes in detail how different societies scaffold a child's learning by gradually increasing the range of difficulty of problems that they encounter.

Mechanisms of development

Neuroconstructivism proposes three underlying, domain-general and level-independent mechanisms. These mechanisms of *cooperation, competition,* and *chronotopy* can be found in some form at multiple levels of description and guide the emergence of partial mental representations. However, the specific way and extent to which these mechanisms are applied varies depending on the level of description (e.g., genes, brain, cognition).

Firstly, ***cooperation*** refers to the notion that there are likely to be multiple contributors to a specific function. For example, multiple genes might contribute cooperatively to support higher-level operations, or at the cognitive level, activity across different domains might be integrated to perform a specific task. In this way, the mechanism of cooperation also allows for the integration of different mental representations that allows for existing knowledge to be re-used at higher levels of functioning.

Secondly, ***competition*** drives the specialisation of components within the system, allowing for greater economy of resources. For instance, where processing becomes progressively realised within one region when it was originally supported by a number of others. Competition is also seen at other levels of description such as gene A inhibiting the expression of gene B, or the competition between neurons for synaptic connectivity, which drives the establishment of more precise connections. As a consequence, more complex representations can be formed through these more specialised connection patterns and areas of function. It is, therefore, the balance of *cooperation* and *competition* which is seen to hinge a given system between a fate of either specialisation or redundancy.

Thirdly, ***chronotopy*** denotes the importance of timing in the process of development. This operates differently across levels of description, but underpins the process of gradual specialisation within a dynamic and adaptive system. At the level of the genome, genes are known to be expressed differentially across developmental time. This is particularly important where a gene may code for a specific low-level process, but that over developmental time interactions with other genes may lead to different developmental outcomes at the cognitive level. Equally, chronotopy is seen to have an effect in adaptive plasticity that occurs across different neural networks and brain regions at different times in development. In sum, the relative timing of events, at different levels of description, is critical for the emergence of neurocognitive function.

Further to these context-dependent mechanisms of *cooperation, competition* and *chronotopy*, Neuroconstructivism suggests that these allow for two central processes that underlie development; and particularly the development of *partial representations* (representations that are just sufficient to drive subsequent behaviour). These processes are *proactivity* and *progressive specialisation*. On the one hand, *proactivity* refers to the role of internally generated activity in the development of function. The notion of proactivity represents the active exploration of the environment by the individual and suggests that the child is not a passive learner. Instead, in a feed-back loop between child and environment, active exploration leads to changes in environmental structure, which in turn has implications for what the child is able to learn from the environment. *Progressive specialisation,* on the other hand, is the gradual process of reduced functional brain plasticity and by which functions (neural, cognitive) become progressively more specific (see Johnson's 2000 notion of Interactive Specialisation).

The nature of mental and neural representations

Fundamental to the Neuroconstructivist approach is the idea of *partial representations*, often modality specific, which are dispersed across a range of brain regions. Rather than suggesting that representations are abstract, amodal, and symbolic structures, as traditional approaches to cognition have often done, Neuroconstructivism argues that representations are embedded within rich networks of existing neighbouring representations. So, for example, the child does not need a whole new symbol to represent a *Dalmatian*. Instead, she only needs to add incrementally to the network of dog knowledge that she already has. Moreover, she only needs to add just enough new information to encode Dalmatians specifically. The Dalmatian part does not "make sense" outside the context of the other existing network of knowledge. Sometimes, the complementary information required to "make sense" of partial information can be found in the structure of the environment, rather than in some complementary neural networks. In this way, knowledge and experience lead to the creation of ever more fragmented and partial representations because they build on a growing network of prior knowledge and experience.

This approach has implications for understanding brain function and the results of neuroimaging studies. Many fMRI studies are based on the idea of subtracting brain activation in two conditions. So, to continue with the example above, when seeking what parts of the brain are involved in representing Dalmatian, researchers might image the child's brain as they look at a picture of a Dalmatian, and subtract from this the activation of the brain when the child looks at pictures of other dogs. This leads to the identification of highly localised areas of activation in the brain: those areas that are only activated by Dalmatians. However, this local specificity is misrepresenting the nature of the representations. It is not just that specific small area that represents the Dalmatian, but a much larger network of common areas that have been subtracted out. Neuroconstructivism argues that the discovery of these highly localised and highly specialised brain areas is a consequence of the subtraction method used to measure brain activity rather than an intrinsic property of neural and cognitive representations.

Testing the Neuroconstructivist Framework: The case of Interactive Specialisation

As touched on above, Interactive Specialisation (IS) is a model of embrainment that includes all the principles and processes of Neuroconstructivism for understanding the role of interactivity in functional brain development (Johnson, 2011). The *Specialisation* term refers to the fact that some regions of cerebral cortex become increasingly fine-tuned to the response properties of particular categories of stimuli (e.g. faces), modes of processing (e.g. number), and task demands, over postnatal developmental time. The *Interactive* term refers to the notion that these patterns of emerging specialisation of regions occur through interaction between different cortical areas, between cortical and subcortical structures, and are influenced by the child's (whole brain) interaction with her social and physical environment. In the original papers discussing Interactive Specialisation we (Johnson 2001, 2011) reviewed longitudinal fMRI imaging and EEG data from multiple domains of perception and cognition such as faces, social cognition, working memory, number, consistent with predictions from the IS framework. It is inherently Neuroconstructivist in the sense that it is centred on the mechanisms of gene-environment interaction. This is contrasted with maturational models in which it is assumed that pre-specified regions come on-line following the unfolding of a genetic programme sensitive only to the biochemical environment, rather than local neural activity induced by the internal or external environment.

Over the past decades a number of authors have attempted to test hypotheses generated from the IS framework. First, while initial support for IS came from the increasing specialisation (or tuning) of individual regions of cortex during human postnatal development, the question remained if IS could be employed to understand how *networks* of different regions, each with their own different specialisations, emerge. Face processing is a good test domain as a "core face network" of cortical regions has been well established in adults, and activity in this network is modulated by task demands in adults (Cohen-Kadosh et al., 2010). A Region-of-Interest (ROI) analysis of the core face network (anterior fusiform gyrus [FG], inferior occipital gyrus [OG], and the superior temporal sulcus [STS]) revealed consistent patterns of co-activation suggesting that these regions are part of a common processing network that responds flexibly in the context of different processing strategies or stimulus changes. Cohen-Kadosh et al. (2010) examined the development of the core face network in younger (7- to 8-years-old) and older (10- to 11-years-old) school-age children as well as young adults, and found that children showed substantially weaker functional connectivity within the face network. More notably, no evidence was found for the influence of task-demands on the effective connectivity within the network in the two children's groups. Thus, both child groups exhibited similar overall network structures, but these weaker networks were not influenced by top-down task demands. Rapid task-specific adaptation may take a decade or more of postnatal experience to emerge, possibly due to the increasing influence of prefrontal cortical areas (Johnson et al., 2009). This approach to understanding the way in which a coherent functional network adjusts and adapts during development to improve task performance is clearly an area of future research focus.

Other authors have set out to test specific developmental predictions of the IS model. For example, Joseph and colleagues (Joseph et al. 2011) also used a face processing task to directly compare IS to a maturational model using fMRI data from children and adults. The key predictions they addressed were:

- Do face-specific regions of cortex respond to face stimuli earlier in development before they become specific to this category of stimuli (demonstrating a process of specialisation) *or* are face-specific regions initially unresponsive to faces (consistent with the activation of a fully formed region from a maturational perspective)?
- In addition to the emergence of cortical areas specific to faces, are there also regressive changes such as decreases in specialisation in other areas (assumed to result from a competitive interaction between different cortical regions to acquire a specialised function).

To assess these hypotheses Joseph et al. identified face-selective *(Footnote that their definition of selective is different – they use "face preferential response")* areas in adults, and they carefully assessed the response properties of the same regions in children. In addition, their analysis methodology using a baseline allowed them to differentiate between areas activated non-selectively (such as one responding equally to both faces and other objects, which they term “conjoined activation”) and non-responsive regions. They also employed a graded specialisation index used in previous studies (Golari et al. 2007). In doing this they found that all face-selective regions in adults had previously been responsive to faces in children (showing conjoined activation), though not necessarily selectively. There were no areas that appeared as fully formed face selective in adults without going through an (inferred) tuning process, consistent with IS. Joseph and colleagues also interpreted their fMRI results as showing both progressive and regressive changes. They defined *Progressive* changes as characterising an area in which the degree of specialisation (for faces) increased with developmental time, whereas *Regressive* changes refers to the response profile becoming *less* specialised over time (i.e., fine to broad tuning). As mentioned above, Joseph and colleagues viewed regressive changes as being key evidence of IS, though this is discussed further below. In accord with their predictions from IS, the authors observed progressive changes in face specialisation in occipital and fusiform areas, and regressive changes in parietal and lateral temporal cortices. While Joseph et al.’s data entirely supported the predictions they generated from the IS framework, their prediction based on the necessity of observing regressive de-specialisation of regions is worthy of further discussion.

Building on this work, and many other studies, Tansey et al. (2024) recently presented a scoping review of evidence for IS in relation to maturation models of visual cortical development. These authors conducted a scoping review of 94 visual developmental fMRI studies across several sub-domains including category-specific visual processing and viewing of natural video scenes. Although inspired by Joseph et al.’s analysis of face processing, the definitions of progressive and regressive developmental events they used were actually much broader, with progressive development defined as “statistically significant increasing association between BOLD contrast magnitude, cluster volume, or selectivity with age” and regressive events similarly broadly defined. These were contrasted with what they termed “emergence”, defined as being a significant response or cluster in an older group that was not present at all in a younger group. IS was considered to have been supported if evidence of both progressive and regressive changes were observed in the same dataset, and a maturational framework was supported if evidence for progressive and emergence changes were reported.

Tansey and colleagues reported strong support for progressive changes across the majority of studies from multiple domains of visual cognition. Thus, their review supported specialisation as a process in functional brain development. In general, the authors conclude there is substantive evidence for progressive changes in “the magnitude, extent, and/or selectivity of the BOLD response” with childhood visual sensory and cognitive development. Overall, there was very little evidence for emergence (the sudden onset of a region with fully formed specificity to a stimulus category), and only some evidence for regressive events in particular domains (face perception, motion, and movies).

According to the authors' analysis, there was thus no evidence for a maturational model and only partial evidence for IS. However, the authors themselves note the limitations of their analysis stating "…findings of progressive or regressive age associations should be considered necessary but not sufficient evidence in support of interactive specialization, as we cannot directly observe competitive interactions and associate plasticity" (Tansey et al., p.2). However, we argue that the insistence on the presence of regressive events (particularly when defined as a "de-tuning" of previously specialised areas) was not a direct prediction of the original IS framework. If we take the example of object and face areas in the ventral visual stream, to our mind IS would predict areas initially responding to a wider range of stimuli (e.g., objects and faces) and then through competitive interaction some areas becoming more specialised on objects and others on faces. The only regressive events that need to occur in this situation are that face areas may come to respond less to objects and vice versa; no de-tuning of other areas is necessarily required. Indeed, under a scenario in which face specialisation emerged due to a selective increase in BOLD response to faces only, and not to other stimuli, no regressive events will be observed at all. Ultimately, however, we agree that the interactive part of IS may be hard to conclusively demonstrate with developmental fMRI (or fNIRS), and may require analyses of directed coherence from EEG or MEG.

A final line of research relevant to the IS framework concerns the relation between functional and structural changes in the cortex during human postnatal development. Kamps and colleagues (Kamps et al., 2020) set out to address the question of whether domain-specific functional cortical networks are preceded by connections that ensure that specificity. In other words, are domain-specific regions (such as those tuned to faces) an inevitable consequence of the brain connectivity that precedes them? Using resting state fMRI in young infants the authors found evidence that cortical networks that grow into later face-specificity and scene-specificity already showed differential input connectivity. Specifically, the authors confirmed our prior knowledge that regions that become face-specific are fed by the foveal projection area of the primary visual cortex, while regions interested in scenes (landscape and city) are differentially fed by the peripheral visual field. While the authors conclude "innate connectivity precedes the emergence of domain-specific function in cortex, shedding new light on the age-old question of the origins of human knowledge" (Kamps et al. 2020), the fact that intrinsic connectivity constrains the nature and domain of representations that emerge within cortical networks has been long incorporated into Neuroconstructivist accounts. For example, Elman et al. (1996) in *Rethinking Innateness* specifically describe 'global architectural constraints' of this kind involving specific patterns of sensory projections that then constrain the kinds of information that can be represented in downstream areas. Furthermore, these constraints are likely to extend to further patterns of connectivity, for example that some face processing areas have multi-modal and motion input as well as reciprocal connectivity to memory systems, making the development of face representations in these areas inevitable (Johnson 2011b). Of course, to paraphrase Piaget – that which is inevitable need not be innate.

Nevertheless, the question of how the specialisation of regions for particular functions shapes brain architecture remains worthy of investigation. In IS a region progresses from responding, but not selectively, to tuning up for a particular category of stimulus. This implies the region already has the appropriate sensory input – with connectivity as described above – but then sharpens its response properties to that category. It is assumed that this sharpening of response properties occurs through some parcellation process involving synaptic or dendritic sculpting to isolate the region from those acquiring other functions. Further, and as discussed above, some process of competitive interaction (potentially through mutual inhibition) could leave one region to "win" over their neighbours.

Extending Neuroconstructivism to incorporate evolution

Neuroconstructivist theory (Mareschal et al., 2007) initially did not incorporate much in the way of genetics (Mareschal et al., 2007a), partly reflecting the state of understanding in the field at that time, although it acknowledged the importance of gene expression and its regulatory factors as a low-level constraint on neurobiological development. Since then, there have been great advances in both the genetics of brain development and of high-level cognitive phenotypes. Advances have been driven by animal work at the level of mechanism and genome-wide association studies in human populations for behavioural and neural phenotypes (e.g., Okbay et al., 2022; Wagstyl et al., 2024; Warrier et al., 2023, Zhou, Song & Ming, 2024). Nevertheless, biological complexity has restricted the development of mechanistic accounts that can span between genetic influences on neurobiological mechanisms and high-level cognitive phenotypes that are the outcome of developmental processes. In line with the neuroconstructivist focus on mechanistic accounts, computational modelling has been used to make progress in building these links (e.g., Thomas, Forrester & Ronald, 2016; Thomas & Coecke, 2023).

Another extension of Neuroconstructivism, which will be the focus of this section, is the connection to evolutionary theory. This continues the Neuroconstructivist tradition of seeking consistency between theories at different levels of description and across different time spans. The original volumes stressed a rejection of David Marr's proposal that accounts of cognition (viewed as computation) and neural circuitry could be characterised at different levels of description that were 'nearly independent' (Marr & Poggio, 1976). Instead, accounts at different levels of description would constrain each other. Stated baldly: you can't have any cognitive theory, it has to be one that can be linked to developmental theory; you can't have any developmental theory, it must be one that can be delivered by the neurobiological processes in the brain; and you can't have any developmental neurobiological theory, it must align with the mechanisms that have been highly conserved across evolution.

The integration of evolutionary theory into Neuroconstructivism will not resemble the old-style evolutionary psychology of the 1990s (e.g., Pinker, 1997; Tooby & Cosmides,1992). That type of evolutionary psychology was driven by cognitive-level theories assuming innate modularity, whose rejection formed a starting point for Neuroconstructivism. We contend that it made no serious contact with biology, rather inferring what must be innate on behavioural and computation grounds; meanwhile, neurobiological genetic influences on brain development although sometimes regionally specific, do not appear to be able to specify cognitive-level content in the cortex. While there are gradients of gene expression that contribute to regionalisation and differentiated cortical structure, these do not correspond neatly to functional areas that map to cognitive functions, and detailed cortical structure is dependent on activity (Cadwell et al., 2019; Elman et al., 1996; Johnson et al., 2011a; Karmiloff-Smith, 1998). High-level cognitive theories based on modularity have now largely fallen out of favour; modularity itself is a notion now more utilised in graph-theoretic approaches to understanding functional and structural brain connectivity (Thomas & Brady, 2021).

In contrast to evolutionary psychology, the integration of evolution into Neuroconstructivist theories builds on the field of evolutionary developmental biology (sometimes called evo-devo; Charvet & Finlay, 2014; Ploeger & Galis, 2011). When applied to the brain, evolutionary theory serves to constrain the theories of functional brain development that in turn are to be reconciled with theories of cognitive development. One challenge of using evolutionary theory in this way is the lack of direct evidence available about how various brain structures and functions evolved. Instead, evidence must be indirect. It involves, variously, comparative studies of brain structure and function across species with different levels of genetic relatedness to infer evolutionary innovation, manipulation of animal models to understand gene function, reconstruction from fossil evidence to trace morphological changes and (for the homo genus) tool use, as well as ecological and geological evidence to infer previous environmental conditions. For example, how evolutionarily old or new a brain structure is can be inferred by the range of species the structure is observed across. Presence across less closely related species implies an evolutionary older common ancestor and therefore an evolutionary older structure. By this measure, subcortical structures such as the amygdala and hippocampus are old within the vertebrate line; while the cortex is similarly old, its large size in humans is new.

In the space available here, we can only give a sketch of what *Evolutionary Neuroconstructivism* will look like. We will lay out some general principles, offer some examples, and then indicate some implications for developmental theory. To emphasise the latter point, the addition of evolution to Neuroconstructivism is not intended to merely add some interesting but optional explanations about how some features of the brain evolved. Rather, because theories in different fields constrain each other, the integration of evolution will ultimately change theories of cognitive development and, as we shall see, lead to an increased focus on what Neuroconstructivism calls *proactivity*, the role of the individual in shaping the experiences that will drive their subsequent functional development.

First the principles. When species are compared – say all mammals or all vertebrates – it appears that biological mechanisms of brain development are highly conserved, both at cellular and anatomical levels. For example, a comparison across mammals indicates that despite very different sizes (say from a mouse to a human), the brains contain similar structures. The size of the structures within the brains of different mammals can be linked by simple patterns of non-linear scaling where, as the whole brain size increases, individual structures become proportionately larger (Charvet, Darlington & Finlay, 2013). This implies that species are using a common plan for growing the brain but scaling it differently (see Shao et al., 2023, for initial work on understanding the genetic basis of this scaling).

While some species show specific behavioural specialisations – say, echolocation in bats, or syntactic language in humans – there are no new large-scale brain structures to reflect these behavioural specialisations. Specific functional brain areas are found underlying these skills in bats and humans, but these fall in predictable areas of sensory, motor, or association cortex and appear to be the outcome of developmental self-organisation (bat echolocation: Bartenstein et al., 2014; Halley et al., 2022; human language: Price, 2012). There are low-level differences in neuronal morphology, neuronal communication, and molecular pathways across species (Shao et al., 2023), but large-scale innovation in evolution appears to be at the periphery rather than in macro brain structure, that is in body morphology, the sensory organs, and musculature; the central nervous system by contrast, remains more general, adapting developmentally to the body it finds itself in (Finlay, Hinz & Darlington, 2011).

Brains differ markedly in size. In part, this follows body size. Brain size scales with body size because a larger body needs more sensory neurons to cover its larger area and more motor neurons to control its larger number of muscle cells. Nevertheless, broadly speaking, a larger brain allows for more behavioural complexity, and this is particularly the case in species that have larger brains even when controlling for body size. Thus, humans have a larger brain for their body size compared to other social primates, supporting their greater behavioural complexity. However, even the components of the human brain scale as expected from the common plan. Part of that scaling is that late developing structures, such as prefrontal cortex, become disproportionately larger as the overall brain size increases. So, while humans have a large prefrontal cortex which permits behavioural complexity, the size is not a specific adaptation; it is what you would expect using the common mammalian growth plan for a brain of that size (Finlay & Uchiyama, 2017).

For evolutionarily old structures, such as the amygdala, hippocampus, and hypothalamus, development is under tight genetic control. For example, the nuclei (components) of the hypothalamus, which coordinates the endocrine (hormone) system, are specified by intrinsic gradients of gene expression during development (Xie & Dorsky, 2017). While the cortex is evolutionarily old, its increased size in humans is new, and this is where plasticity plays a greater role in establishing functional structures. Primary sensory inputs and motor outputs are under strong genetic specification, but experience-dependent self-organisation reinforces the functional specialisation of some higher-order regions (as featured in IS). Importantly, computational modelling has demonstrated that if the primary sensory inputs to the cortical sheet are conserved, as are its principles of self-organisation, but the size of the sheet is scaled up, self-organisation alone will produce more functionally specialised regions across development (Imam & Finlay, 2020). This demonstrates that increased complexity as a developmental outcome can be produced merely by scaling, given conserved mechanisms of self-organisation and experience-dependent processes.

The generality of the cortex – that is, its lack of commitment to particular content for a given species – can be demonstrated by genetic manipulation. For example, mouse vision is dichromatic, based on two colours. In the retina of mouse eyes, there are detectors for blue and yellow light, but none for red. No mouse has ever seen red. However, with modern genetic methods, it is possible to create a new breed of mice which have additional detectors in their retinas for red light (Jacobs et al., 2007). (Genes code for proteins, and specific proteins in light detectors in the retina vibrate in response to a certain wavelength of light. If you alter the relevant gene, you can change the structure of the protein, and this can alter the wavelength of light that will cause it to vibrate.) The brains of these new growing mice now receive sensory information about red light from their environment that their species has never before received. Can the mouse cortex develop sensory representations using input from the red-light receptors to drive behaviour? Yes, it can. Representational content is flexible to changes in sensory input even beyond those that have previously occurred in the species.

At the level of neurons, early developmental conditioning appears to confer neuronal identities for motor versus sensory areas. However, neurons have been transplanted between sensory areas in very young animals, for example from visual to somatosensory areas, and found to take on the computational properties in the new region (see Cadwell et al., 2019, for review). Once more, the evidence points to plasticity as a key factor for representational content in the cortex.

The conservation of vertebrate brain anatomy brings us to a puzzle, however. Species can show quite different behavioural repertoires, for example in their social behaviour and social structures, even when their brain anatomies appear very similar. If mammals have similar brain plans, mainly varying in size, where do the species-specific functional differences come from? Why do wolves hunt and sheep flock? The special abilities of each species are likely to come from four main sources (Finlay, Hinz & Darlington, 2011). First, the sensory and motor periphery impose their form on the central nervous system: the mole's whiskers, the bat's tongue and ears, the human's dextrous digits. Second, changes in the chemistry of the brain, including neurotransmitters and hormones, alter the social motivations, desired rewards, and attentional focus of the species – the social or physical environments they want to be in, the experiences they want to have, the conspecifics with whom they want to affiliate. Third, the cortex is plastic. Within some limits, it dynamically reallocates its neural tissue according to its experiences and motivational preferences. Fourth, overall brain size varies across species. With more neural "real estate", more complex representations can be developed.

Mammalian brains contain a range of structures that influence the behaviours that individuals are likely to initiate, the situations they are likely to encounter, and the experiences they will find rewarding. Table 1 shows some of these structures for humans. Some are cortical but most are subcortical. If these structures are tuned differently, via neuromodulation or connectivity, the result is an individual which chooses actions that are more or less likely to lead to certain kinds of rewards or experiences; more or less likely to approach, avoid, or tolerate certain situations; more or less likely to make decisions based on emotional states versus plans and goals; and more or less likely to respond to other members of the species in a receptive manner (Canli, 2006).

Table 1. Brain regions that when tuned differently (across species or within species) lead to differences in proactivity, including approach, avoidance and tolerance behaviour, arousal, novelty seeking, threat detection, sociality, territorial defence, sensitivity to rewards, and stress response. Tuning may occur through neurohormonal and neurotransmitter modulation, or altered patterns of connectivity (from Thomas & Green, 2023).

Region	**Function**
Cortical	
Dorsolateral prefrontal cortex	Decision making around sensorimotor and control, cognitive flexibility, inhibition
Dorsomedial prefrontal cortex	Decision making around social behaviour
Ventromedial prefrontal cortex	Decision making around emotions / emotion regulation
Orbitofrontal cortex	Decision making around anticipated reward and punishment
Sub-cortical	

Amygdala	Appetites: detect social cues / threat cues / novelty cues to trigger approach-avoidance behaviour
Insula	Bodily basis of empathy, tendency to feel disgust
Anterior cingulate	Monitoring of state against goals (including pain)
Nucleus accumbens	Detecting / seeking pleasure
Habenula	Detecting disappointments, missing rewards
Septum	Social affiliative behaviour, attachment
Basal ganglia (striatum)	Predicting rewards/punishments in order to select actions
Hippocampus	Storing sensory spatial information for where emotionally salient events occurred; novelty detection
Hypothalamic-Pituitary-Adrenal (HPA) axis	Regulation of stress response

Here are two examples from comparative studies. The prairie vole and the montane vole are closely related species of small rodent which show diverse bonding behaviours. The prairie vole is monogamous (one stable mating relationship between a male and a female), while the montane vole is polygamous (multiple partners). Nevertheless, the two species have very similar brain anatomy. A key evolutionary lever to alter behavioural repertoire appears to be changes in the distribution in neural structures of receptors for oxytocin, a hormone involved the mediation of several forms of affiliative behaviour including parental care, grooming, and sex behaviour (Matthews, Williams & Schweiger, 2013). The two species show differential distribution of receptors for this hormone, both in appetitive structures and in reward structures (Insel & Shapiro, 1992). Changes in receptor distribution between the species both alter the bonding behaviours the animals are likely to initiate and the rewards they experience from those situations, creating the history of experiences that shape future developmental trajectories (see Thomas & Green, 2023, for discussion).

A recent comparison by Qi et al. (2023) across Asian colobine primates, a set of closely related monkey species, explored the genetic differences associated with variations in the complexity of social systems across related species of monkey. These social systems span from solitary living to one-male-multiple-female family groups to large multi-level societies. The study concluded that more complex social systems emerged in species that were adapted to cold climates, where co-operative behaviour is more important for survival. However, the same social systems continued even when the species moved to occupy warmer climates, suggesting the social complexity was a heritable trait rather than driven by features of the immediate environment. Reconstruction of speciation events and genomic analysis suggested that the increase in social complexity was triggered through selection of gene variants to promote maternal care in nurturing babies in cold conditions. Glacial periods promoted the selection of genes involved in cold-related energy metabolism and neurohormonal regulation. More efficient dopamine and oxytocin pathways had evolved in the species of monkeys with more complex social systems. While this neurohormonal modulation may have favoured the prolongation of maternal care and lactation, thereby increasing infant survival in cold environments, the adaptive changes also appeared to strengthen inter-individual affiliation. This increased male-male tolerance and facilitated the stepwise aggregation from independent one-male groups to large multilevel societies. Again, in this example, we see how the tuning of appetitive and reward systems is involved in driving the emergence of complex behaviour without major changes in neuroanatomy.

One might view this as interesting but not directly relevant to human development. However, the evolutionary conservation of mechanisms suggests that variation within species is likely to be of the same kind as variation between species. This is likely since new species arise from genetic variation that occurred within previous species, but there is also direct evidence. We saw how the size of different brain structures scales reliably with overall brain size across species. For example, the pattern holds in comparing the size of brain structures and overall brain size across macaque monkeys, chimpanzees, and humans (Donahue et al., 2018). Differences in brain size can also be found between humans; and these within-species differences have been observed to follow the same scaling principles as those observed across species (Finlay, 2019). Thus, in the dataset that compared macaques, chimpanzees, and humans, the late developing prefrontal cortex scaled with overall grey matter volume at a faster rate than a primary sensory area like V1; this scaling relationship was observed across the three species; and crucially, variation between individuals within each species held to the same relationship (Donahue et al., 2018).

The link between between-species variation and within-species variation suggests on the one hand that insights gained from understanding the development of different behavioural repertoires across species are likely to shed light on the origin of behavioural differences among humans; and on the other hand, that the biological mechanisms conserved by evolution will constrain explanations of underpinning neurobiological processes in human brain development. One may, therefore, re-reread the preceding paragraph on the puzzle of the origin of differences between species as also addressing the puzzle of the origin differences between people. Rather than individual differences between people being explained by variation in brain structure at the macro level, the same four sources of difference are likely to apply: the sensory and motor periphery will impose their form on the central nervous system; changes in the chemistry of the brain will modulate proactivity through motivations, attention, and reward; plasticity will dynamically reallocate neural tissue across development according to experiences and motivational preferences; and, for typical development, overall brain size will vary between individuals influencing behavioural complexity.

This has the following implications for the theory of Neuroconstructivism. First, interactive specialisation is an underpinning principle of functional brain development, but this mainly applies to development of the cortex. Experience-dependent self-organisation appears to be a more important factor in the development of functionally specialised regions in the cortex, while the regional development of sub-cortical structures is under tighter genetic control. We also need a subcortical focus to understand the *proactivity* element of Neuroconstructivism. Second, macro scale brain structure differences (outside of genetic syndromes) may not be the most informative place to look for differences in developmental outcomes. Instead, we need to consider lower-level factors such as neurotransmitters and neurohormones. These alter motivational and reward systems that shape behaviour and therefore the experiences that drive development (and *Interactive Specialisation* in the cortex). The study of appetitive and reward differences in neurodevelopmental conditions, especially those showing differential social approach/avoidance preferences, is an important future direction, since overt differences in neuroanatomy are rarely found for behaviourally defined conditions. Third, overall brain size is important for behavioural complexity across species (Reader, Hager & Laland, 2011), and this will likely be one element of human general intelligence, as indeed suggested both by large-scale correlational data in human populations and by genetic analyses supporting the causal role of brain size on intelligence (e.g., Jansen et al., 2020; Lee et al., 2019; Nave et al., 2019).

We may reflect on how an evolutionary perspective further defines or complements the core neuroconstructivist principles of encellment, embrainment, embodiment, and ensocialment. The perspective adds constraints to developmental theory: on the one hand, developmental mechanisms that are conserved across species suggest those that may underpin human development; on the other hand, mechanisms that are readily tuneable to produce behavioural differences in developmental outcomes across species are candidates for those that produce individual differences between humans.

With respect to encellment, Finlay and Uchiyama (2015) report that across species, there is a disparity in neuron number in each cortical column along a rostrocaudal axis which grows with cortical size. Along with a difference in the patterns of axon extension and synaptogenesis along the same axis, these differences may produce a progressive amplification of hierarchical processing as brains become larger, supporting greater behavioural complexity. Hierarchical processing supports concept development from sensory information, action planning from motor sequence information, and control processes for behavioural flexibility, goal-oriented behaviour, and decision making.

With respect to embrainment, a structure can take on new functions using plasticity if the function of other systems within which it is embedded alters, for example, as facilitated by their greater size. This may lead to altered division of labour among structures, such as, for example, dorsal versus ventral routes for using sensory information to drive behaviour. Plasticity may also allow adaptive goals to be met in the face developmental anomalies in sensory or motor systems (Johnson, Jones & Gliga, 2015); or for the operation of more complex cognitive control systems to shape the development of sensory systems, such as through selective attention (Amso & Scerif, 2015).

With respect to embodiment, the plasticity of the central nervous system allows the same structure to produce different functions when embodiment is altered, or new embodied experiences become available (such as, say, the use of thumbs for texting with the invention of smart phones). Prefrontal cortex may be particularly important in adapting to the local ecology due to its protracted course of development (Werchan & Amso, 2017).

Lastly, with respect to ensocialment, motivation and reward tendencies can only shape experiences (and through them, developmental outcomes) if the environment provides contingencies to generate new experiences and gain new rewards. Cultures, including the innovative social settings, niches and toolsets they create, may provide new opportunities for behaviours that will provide rewards triggering both functional development and affective states. In contemporary culture, social media is an obvious candidate, providing social rewards or punishments in views and comments on a social media posts with the invention of the internet and handheld devices, triggering new behavioural repertoires of online activity, and sometimes subsequent changes in wellbeing (e.g., Girela-Serrano et al., 2024).

The conclusion from this section is that advances in Neuroconstructivist theory point to an extension of its initial requirement – that theories of cognitive development should be consistent with theories of functional brain development – to the requirement that theories of functional brain development should be consistent with how we understand genes to influence brain development; and that neurobiological theories of development should be consistent with mechanisms that appear to be highly conserved across species. Complementary to the central role that *Interactive Specialisation* played in explaining cortical development within the original formulation of Neuroconstructivism, *Evolutionary Neuroconstructivism* points towards a greater investigation of the role of subcortical structures and neurohormonal modulation in driving the proactivity that fashions the functional development of the cortex.

Conclusion

The Neuroconstructivist framework underscores the fundamental importance of *interactions* in development. These interactions operate at all levels of representation from -- cells to individuals to societies. This influential framework has shaped the thinking of developmental scientists over the last 20 years and continues to do so when thinking about both typical and atypical development. The Neuroconstructivist framework also affords testable hypotheses; recent work focusing on the *Interactive Specialisation* dimension has largely been confirmatory, although some elements of the framework (such as the presence of regressive events) need further investigation. Since the original publication of the Neuroconstructivist volumes, developments in our understanding of genes and the context dependence of gene-expression have allowed us to generalise the Neuroconstructivist framework to include genetic level descriptions within this dynamic-interactive framework. In this chapter, we have also explored how evolutionary pressures that contribute to the emergence of the developmental mechanisms identified in young children can also be incorporated within the framework. A full understanding of the mechanisms and processes involved in development involves not just focusing on the interactivity but also including all mechanistic levels of interaction such as genes and the evolutionary antecedents of current human development identified through cross species comparisons of development and behaviour. The evolutionary perspective (newly introduced in this chapter) stresses the importance of proactivity, consistent with the points raised in the introduction about how the child's behaviour drives the experiences that produce emergent specialisation in the brain.

The overarching aim of this volume is to explore the interactions of learning, memory and attention in early child development. This aim can be viewed as a canonical case study in how the Neuroconstructivist principles can help us understand these interactions. As discussed in Section 3 of this volume, learning, memory and attention are largely indissociable. Context shapes how these processes interact throughout development. Indeed, the whole of Section 6 focuses on how context and individual differences in experiences shape the intimate interactions between learning, memory and attention, in line with the arguments made here. In this chapter cross-species comparisons are essential for understanding the current processes of development, and Section 5 of this volume presents evidence from a range of different species that is relevant to understanding early development.

Also at the heart of the Neuroconstructivist approach is the idea that an understanding of phenomena requires construction of a causal mechanistic framework. Mechanisms are theoretical constructs that allow us to predict the future state of the developing individual either in instantaneous time or across developmental time as a function of their current and previous states. This is critical if we want to be able to intervene when development goes awry or to support and enhance more effective development. Computational models implemented through simulations provides a tool for exploring the effectiveness of the putative mechanisms. Behavioural neuroimaging and genetic studies provide the input constraints that allow us to develop these computational models. The models allow us to clarify precisely what general terms such as attention learning in memory might mean in the context of specific substrates and specific levels of representation. Indeed, while there have been centuries of debates about the nature of attention, memory and learning the meaning of these words has shifted with time as our understanding of behaviour has evolved. Agreeing on clear operational definition of these terms is a necessary requirement for understanding their interactive co-development.

References

Amso D, Scerif G. The attentive brain: insights from developmental cognitive neuroscience. *Nat Rev Neurosci.* 2015 Oct;16(10):606-19. doi: 10.1038/nrn4025. PMID: 26383703; PMCID: PMC4885514.

Astle, D. E., Johnson, M. H., & Akarca, D. (2023). Toward computational neuroconstructivism: a framework for developmental systems neuroscience. *Trends Cogn Sci.* 2023 Aug;27(8):726-744. doi: 10.1016/j.tics.2023.04.009.

Astle, D. E., Bassett, D.S., Viding, E. (2024). Understanding divergence: Placing developmental neuroscience in its dynamic context, *Neuroscience & Biobehavioral Reviews, 157,* 105539, https://doi.org/10.1016/j.neubiorev.2024.105539

Bartenstein, S., Gerstenberg, N., Vanderelst, D. et al. (2014) Echo-acoustic flow dynamically modifies the cortical map of target range in bats. *Nat Commun 5*, 4668, https://doi.org/10.1038/ncomms5668

Bennardo, G. (2024). Cultural Model Theory: Culture, Mind, and Knowledge. In: Bennardo, G., de Munck, V.C., Chrisomalis, S. (eds) *Cognition In and Out of the Mind. Culture, Mind, and Society*. Palgrave Macmillan, Cham. https://doi.org/10.1007/978-3-031-48181-9_1

Bettoni R, Cantiani C, Riboldi EM, Molteni M, Bulf H, Riva V (2024) Visual statistical learning in preverbal infants at a higher likelihood of autism and its association with later social communication skills. PLoS ONE 19(5): e0300274. https://doi.org/10.1371/journal.pone.0300274

Cadwell CR, Bhaduri A, Mostajo-Radji MA, Keefe MG, Nowakowski TJ. Development and Arealization of the Cerebral Cortex. *Neuron*. 2019 Sep 25;103(6):980-1004. doi: 10.1016/j.neuron.2019.07.009.

Canli, T. (2006). *Biology of personality and individual differences*. Guilford Press.

Champagne, F. A. & Curley, J. P. (2005) How social experiences influence the brain. *Current Opinion in Neurobiology, 15*, 704-709.

Charvet, C. J., Darlington, R. B., & Finlay, B. L. (2013). Variation in Human Brains May Facilitate Evolutionary Change toward a Limited Range of Phenotypes. *Brain Behav Evol*, 81 (2): 74–85.

Charvet, C. J., & Finlay, B. L. (2014). Evo-devo and the primate isocortex: the central organizing role of intrinsic gradients of neurogenesis. *Brain Behav Evol*. 2014;84(2):81-92. doi: 10.1159/000365181.

Clark, A. (1997). *Being there: putting brain, body and world together again*. Cambridge, Massachusetts: MIT Press.

Crone, E. A., & Dahl, R. E. (2012) Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nat Rev Neurosci*. 2012 Sep;13(9):636-50. doi: 10.1038/nrn3313.

Donahue, C. J., Glasser, M. F., Preuss, T. M., Rilling, J. K., & Van Essen, D. C. (2018). Quantitative assessment of prefrontal cortex in humans relative to nonhuman primates. *Proc Natl Acad Sci USA*. 2018 May;115(22):E5183–92.

Elman, J., Bates, E., Johnson, M.H**.**, Karmiloff-Smith, A., Parisi, D, and Plunkett, K. (1996) *Rethinking Innateness: A Connectionist Perspective on Development*. Cambridge, MA: MIT Press.

Finlay, B. L. (2019). Generic Homo sapiens and Unique Mus musculus: Establishing the Typicality of the Modeled and the Model Species. *Brain Behavior and Evolution*, 93, 1-15. https://doi.org/10.1159/000500111.

Finlay, B. L., Hinz, F., & Darlington, R. B., (2011). Mapping behavioural evolution onto brain evolution: the strategic roles of conserved organization in individuals and species. *Phil. Trans. R. Soc.* B3662111–2123. http://doi.org/10.1098/rstb.2010.0344

Finlay, B. L., & Uchiyama, R. (2015). Developmental mechanisms channeling cortical evolution. *Trends in Neurosciences*. Volume 38, Issue 2, February 2015, Pages 69-76. https://doi.org/10.1016/j.tins.2014.11.004

Finlay, B.L., Uchiyama, R. (2017). The Timing of Brain Maturation, Early Experience, and the Human Social Niche. In: Kaas, J (ed.), *Evolution of Nervous Systems* 2e. vol. 3, pp. 123–148. Oxford: Elsevier.

Girela-Serrano, B.M., Spiers, A.D.V., Ruotong, L. et al. (2024). Impact of mobile phones and wireless devices use on children and adolescents' mental health: a systematic review. *Eur Child Adolesc Psychiatry* 33, 1621–1651 (2024). https://doi.org/10.1007/s00787-022-02012-8

Gottlieb, G. (2007). Probabilistic epigenesis. *Developmental Science, 10*, 1-11.

Halley, A. C., Baldwin, M. K. L., Cooke, D. F., Englund, M., Pineda, C. R., Schmid, T., Yartsev, M. M., & Krubitzer, L. (2022). Coevolution of motor cortex and behavioral specializations associated with flight and echolocation in bats. *Current Biololgy,* 32(13):2935-2941 doi: 10.1016/j.cub.2022.04.094.

Imam N., & Finlay, B. L. (2020). Self-organization of cortical areas in the development and evolution of neocortex. *Proc Natl Acad Sci U S A*., 117(46):29212-29220. doi: 10.1073/pnas.2011724117.

Insel, T. R., & Shapiro, L. E. (1992). Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. *Proc Natl Acad Sci U S A*., 89(13):5981-5. doi: 10.1073/pnas.89.13.5981.

Jacobs, G. H., Williams, G. A., Cahill, H. & Nathans, J. (2007). Emergence of novel color vision in mice engineered to express a human cone photopigment. *Science* 315, 1723–1725. doi:10.1126/science.1138838

Jansen, P. R., Nagel, M., Watanabe, K. et al. (2020). Genome-wide meta-analysis of brain volume identifies genomic loci and genes shared with intelligence. Nat Commun 11, 5606 (2020). https://doi.org/10.1038/s41467-020-19378-5

Johnson, M.H. (2000) Functional brain development in infants: Elements of an interactive specialization framework. *Child Development, 71,* 75-81.

Johnson, M.H. (2011a) Interactive Specialization: A domain-general framework for human functional brain development? *Developmental Cognitive Neuroscience*. doi: 10.1016/j.dcn.2010.07.003

Johnson, M.H. (2011b) Face processing as brain adaptation at multiple time scales. *Quarterly Journal of Experimental Psychology, 64,* 1873-1888.

Johnson MH, Charman T, Pickles A, Jones EJH. (2021) Annual Research Review: Anterior Modifiers in the Emergence of Neurodevelopmental Disorders (AMEND)-a systems neuroscience approach to common developmental disorders. *J Child Psychol Psychiatry*, 62(5):610-630. doi: 10.1111/jcpp.13372.

Johnson MH, Jones EJ, Gliga T. (2015). Brain adaptation and alternative developmental trajectories. Dev Psychopathol. 2015 May;27(2):425-42. doi: 10.1017/S0954579415000073. PMID: 25997763.

Joseph et al. (2011) Progressive and regressive developmental changes in neural substrates for face processing: Testing specific predictions of the Interactive Specialization account. *Developmental Science, 14*, 227-241.

Kamps FS, Hendrix CL, Brennan PA, Dilks DD. Connectivity at the origins of domain specificity in the cortical face and place networks. *Proc Natl Acad Sci U S A*. 2020 Mar 17;117(11):6163-6169. doi: 10.1073/pnas.1911359117.

Karmiloff-Smith A. (1998) Development itself is the key to understanding developmental disorders. *Trends Cogn Sci*. 2(10):389-98. doi: 10.1016/s1364-6613(98)01230-3.

Karmiloff-Smith, A. (2009). Nativism versus neuroconstructivism: rethinking the study of developmental disorders. *Developmental Psychology, 45*, 56.

Lee, J. J., McGue, M., Iacono, W. G., Michael, A. M., & Chabris, C. F. (2019).The causal influence of brain size on human intelligence: Evidence from within-family phenotypic associations and GWAS modeling. *Intelligence*. 2019 Jul-Aug;75:48-58. doi: 10.1016/j.intell.2019.01.011.

Mareschal, D., Johnson, M., Sirios, S., Spratling, M., Thomas, M. S. C., & Westermann, G. (2007) Neuroconstructivism: How the brain constructs cognition. Oxford, UK: Oxford University Press.

Mareschal, D. & Thomas, M. S.C. (2007) Computational modeling in developmental psychology. *IEEE Transactions on Evolutionary Computation* 11 (2), pp. 137-150.

Marr, D., and Poggio, T. (1976). *From Understanding Computation to Understanding Neural Circuitry.* Artificial Intelligence Laboratory. A.I. Memo. Massachusetts Institute of Technology. AIM-357. Retrieved from dspace.mit.edu/handle/1721.1/5782.

Matthews, T. J., Williams, D. A., & Schweiger, L. (2013). Social Motivation and Residential Style in Prairie and Meadow Voles. *The Open Behavioral Science Journal* 7:925001. https://doi.org/10.2174/1874230020130925001

Mechelli, A., Price, C. J., & Friston, K. J. (2001). Nonlinear coupling between evoked rCBF and BOLD signals: a simulation study of hemodynamic responses. *NeuroImage, 14*, 862-872.

Mercer, A. R. (2001). The predictable plasticity of honey bees. In Christopher A. Shaw, Jill McEachern (Eds.) *Towards a theory of neuroplasticity*. Psychology Press. https://doi.org/10.4324/9780203759790

Nave G, Jung WH, Karlsson Linnér R, Kable JW, Koellinger PD. (2019) Are Bigger Brains Smarter? Evidence From a Large-Scale Preregistered Study *Psychological Science, 30*, 43-54. doi: 10.1177/0956797618808470.

Oakes L. M. (2023). The development of visual attention in infancy. In Tamis-LeMonda C., Lockman J. J. (Eds.), *Advances in child development and behavior: Developmental cascades* Vol. 64,(pp. 1–37). Elsevier.

Okbay, A., Wu, Y., Wang, N. et al. (2022). Polygenic prediction of educational attainment within and between families from genome-wide association analyses in 3 million individuals. *Nat Genet* 54, 437–449. https://doi.org/10.1038/s41588-022-01016-z

Perry, R. C., Johnson M., Charman, T., Pascoe, G., Thomas, M. S. C., Tolmie, A., Dumontheil, I., Jones, E. J., & The BASIS Team (2024). Twenty-four-month effortful control predicts emerging autism characteristics. *Developmental Science*.

Piaget, J. (1970). *Genetic epistemology* (E. Duckworth, Trans.). New York: Columbia University Press.

Pinker, S. (1997). *How the mind works*. New York, NY: W. W. Norton & Company.

Ploeger, A., & Galis, F. (2011). Evo Devo and cognitive science. *WIREs Cognitive Science*, 2(4), 429–440. https://doi.org/10.1002/wcs.137

Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *Neuroimage, 15*, 62, 816-47. doi: 10.1016/j.neuroimage.2012.04.062.

Reader SM, Hager Y, Laland KN. (2011) The evolution of primate general and cultural intelligence. Philos Trans R Soc Lond B Biol Sci., 366, 1017-27. doi: 10.1098/rstb.2010.0342

Qi XG, Wu J, Zhao L, Wang L, Guang X, Garber PA, Opie C, Yuan Y, Diao R, Li G, Wang K, Pan R, Ji W, Sun H, Huang ZP, Xu C, Witarto AB, Jia R, Zhang C, Deng C, Qiu Q, Zhang G, Grueter CC, Wu D, & Li B. (2023). Adaptations to a cold climate promoted social evolution in Asian colobine primates. *Science*, 380(6648):eabl8621. doi: 10.1126/science.abl8621

Rogoff, B. (2003). *The Cultural Nature of Human Development*. New York: Oxford University Press.

Sadato, N., Pascual-Leone, A., Grafman, J., & Ibañez, V. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. *Nature, 380,* (6574), 526.

Saragosa-Harris, N. M., Cohen, A. O., Reneau, T. R., Villano, W. J., Heller, A. S., & Hartley, C. A. (2022). Real-World Exploration Increases Across Adolescence and Relates to Affect, Risk Taking, and Social Connectivity. *Psychological Science*, 33(10), 1664-1679. https://doi.org/10.1177/09567976221102070

Shao Y, Zhou L, Li F, Zhao L, … & Wu DD. (2023). Phylogenomic analyses provide insights into primate evolution. *Science*. 2023 Jun 2;380(6648):913-924. doi: 10.1126/science.abn6919.

Tansey et al. (2024) Development of human visual cortical function: A scoping review of task- and naturalistic – fMRI studies through the interactive specialization and maturational frameworks. *Neuroscience and Biobehavioral Reviews, 162*

Thomas, M. S. C. & Green, S. (2023). *How the brain works*. London, UK: Sage Publishers.

Thomas, M. S. C., & Brady, D. (2021). Quo vadis modularity in the 2020s? In M. S. C. Thomas, D. Mareschal, & V. Knowland (Eds.), *Taking development seriously: A festschrift for Annette Karmiloff-Smith: Neuroconstructivism and the multi-disciplinary approach to understanding the emergence of mind* (pp. 159–173). Routledge/Taylor & Francis Group.

Thomas, M. S. C., & Coecke, S. (2023). Associations between socioeconomic status, cognition and brain structure: Evaluating potential causal pathways through mechanistic models of development. *Cognitive Science*, 47(1), e13217. https://doi.org/10.1111/cogs.13217

Thomas, M. S. C., Forrester, N. A., & Ronald, A. (2016). Multi-scale modeling of gene-behavior associations in an artificial neural network model of cognitive development. *Cognitive Science*, 40(1), 51-99. DOI: 10.1111/cogs.12230.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds*.), The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York, NY: Oxford University Press

Turkewitz, G., & Kenny, P. A. (1982). Limitations on input as a basis for neural organization and perceptual development: A preliminary theoretical statement. *Developmental Psychobiology, 15*, 357-368.

Wagstyl, K., Adler, S., Seidlitz, J., Vandekar, S., Mallard, T. T., Dear, R., DeCasien, A. R., Satterthwaite, T. D., Liu, S., Vértes, P. E., Shinohara, R. T., Alexander-Bloch, A., Geschwind, D. H., & Raznahan, A. (2024). Transcriptional cartography integrates multiscale biology of the human cortex. *eLife* 12:RP86933. https://doi.org/10.7554/eLife.86933.3

Warrier, V., Stauffer, EM., Huang, Q.Q. et al. (2023). Genetic insights into human cortical organization and development through genome-wide analyses of 2,347 neuroimaging phenotypes. *Nat Genet* 55, 1483–1493 (2023). https://doi.org/10.1038/s41588-023-01475-y

Wass, S. V. (2021) The origins of effortful control: How early development within arousal/regulatory systems influences attentional and affective control, *Developmental Review, 61*, 100978, https://doi.org/10.1016/j.dr.2021.100978.

Werchan DM, Amso D. (2017). A novel ecological account of prefrontal cortex functional development. *Psychol Rev.* 2017 Nov;124(6):720-739. doi: 10.1037/rev0000078.

Westermann, G., Mareschal, D., Johnson, M. H., Sirois, S., Spratling, M. & Thomas, M. S.C. (2007) Neuroconstructivism. *Developmental Science* 10 (1), 75-83.

Westermann, G. and Sirois, S. and Shultz, T.R. and Mareschal, D. (2006) Modeling developmental cognitive neuroscience. *Trends in Cognitive Sciences* 10 (5), pp. 227-232. ISSN 1364-6613.

Whitfield, C.W., Cziko, A.M. and Robinson, G.E. (2003) Gene Expression Profiles in the Brain Predict Behavior in Individual Honey Bees. *Science*, *302*, 296-299. http://dx.doi.org/10.1126/science.1086807

Xie Y, Dorsky RI. (2017). Development of the hypothalamus: conservation, modification and innovation. *Development*. 2017 May 1;144(9):1588-1599. doi: 10.1242/dev.139055. PMID: 28465334; PMCID: PMC5450842.

Zhou, Y., Song, H., & Ming, G. L. (2024). Genetics of human brain development. *Nat Rev Genet.* 2024 Jan;25(1):26-45. doi: 10.1038/s41576-023-00626-5. Epub 2023 Jul 28. PMID: 37507490; PMCID: PMC10926850.