Neural process models can help keep theory at the forefront of developmental neuroscience.

Commentary on Marshall, Arsalidou, Rueda, Crone & van Drunen.

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Abstract

We discuss the four chapters in this special issue, focusing on three key questions: (1) what developmental theories are being used across chapters; (2) what neuroscience methods are being used; and (3) how are these integrated? We organise our discussion by chapter moving from the broadest conceptual chapter by Peter Marshall through to the integration of theory and methods by Crone and van Drunen. We end by discussing work that is missing from the special issue that uses neural process models to integrate developmental theory with cognitive neuroscience methods. We highlight how this approach can yield a tighter integration between theory and methods, enabling researchers to test specific hypotheses about the mechanisms that underlie change in development. We suggest that this approach might prove to be a particularly effective way to keep theory at the forefront of developmental neuroscience.

The goal of this special issue was to obtain a broad sampling of how theory is informing work across various areas of developmental neuroscience. The authors were asked to consider the following set of framing questions: (1) how has the integration of neuroscience methods with developmental theory advanced the field's understanding of developmental processes; (2) how do you conceptualize development and developmental processes within your own research; (3) how has developmental theory driven your research questions, shaped the kinds of questions you have asked, and informed interpretations of your findings; and (4) what are several key guiding principles that should inform developmental neuroscience work so that theory stays at the forefront of our scientific inquiries?

The target chapters addressed these questions in diverse ways, with each paper focusing on a different topic ranging from the evolution of the brain to a neo-Piagetian view of concept development to attention development in infancy to the development of the self-concept. As such, commentating on this collection was quite a challenge. We decided to focus on a smaller set of questions that we hope will shed light on the central theme of the collection: how to keep theory at the forefront of developmental neuroscience? Our questions were as follows: (1) what developmental theories are being used across chapters; (2) what neuroscience methods are being used; and (3) how are these integrated? We organise our discussion by chapter moving from the broadest conceptual chapter by Peter Marshall through to the elegant integration of theory and methods by Crone and van Drunen.

Brain evolution constrains brain development, but the devil is in the details. We begin with the chapter by Marshall as he presents a broad conceptual overview of how brain development is constrained by brain evolution. Marshall's central premise is that the brain must be conceptualised in the context of evolution and evidence that the brain evolved to serve sensori-motor systems. Thus, we need to always think about the brain in the context of action and the goals of the organism. Marshall contrasts this view with a common conceptualisation of the brain as a computational device that passively processes input. This passive view is commonly adopted in information processing perspectives. A good example comes from recent work that uses convolutional neural networks to classify images (Krizhevsky et al., 2012). Here, static images are presented to the network and a classification decision is made. Little attention is given to the goals of the organism. Consequently, there are no spatial-temporal patterns in the input which would be produced by a mobile organism. Similarly, classification decisions are not actively maintained by the network. Rather, the neural patterns in the network are one-shot computations without the recurrency needed to maintain patterns over time to support actions in context (for discussion, see Schöner, 2023). Thus, by giving the network a large set of static images, recent work has created an artificial brain that bears little resemblance to how the brain works in real, mobile, dynamic organisms.

To illustrate an alternative approach, Marshall focuses on the example of building a body map in cortex in early development. Here, Marshall describes EEG and MEG patterns of activity that demonstrate somatotopy through associations with tactile body part stimulation. Marshall suggests these body maps develop prenatally and are involved in the underpinnings of social engagement as EEG patterns demonstrate infants may have a felt similarity between their own body representation and that of others. Marshall suggests this is the result of self-generated bodily activity that begins prenatally, citing research on the tactile stimulation present within the intrauterine social environment. The idea is that spontaneous activity generates spatial-temporal patterns which then shape cortical maps, likely through associative processes. Here, however, Marshall shies away from such explanations as they tend to lead to contrasting genetic versus experience-dependent (i.e., associative) processes which he thinks is a theoretical cul-du-sac. While we agree that researchers often contrast such views, shying away from associative mechanisms does not seem to be a good way forward as the brain is fundamentally an associative organ. The alternative, we contend, is to think clearly about associations – which can do quite amazing things – but to also think clearly about the role of genes in development. For instance, we know that genes are differentially expressed as a function of differential experience (Gibney & Nolan, 2010); thus, rather than treating genes as one source of developmental change and associations as a different source, we need to understand how gene expression and associative processes might work together through time. In short, we agree that the field needs more sophisticated thinking about the role of genes in development, but we do not agree that this necessitates shying away from associative mechanisms.

We conclude this section with our three questions. First, what theory is Marshall using? He is using developmental systems theory to frame his discussion of brain development. What methods is he using? Much of Marshall’s evidence comes from studies of animal brain development, although there is some discussion of EEG and MEG when he gets into the formation of body maps in infancy. Finally, how are these integrated? The integration here is vague: on one hand, Marshall points toward evidence of associative learning, but on the other hand, he is not clear about where associative processes sit in terms of an embodied, developmental systems perspective.

Mapping a neo-Piagetian perspective onto the brain. The next chapter we discuss is the chapter by Arsalidou. Here, the theoretical approach is explicitly neo-Piagetian. The chapter discusses a theory of constructive operators proposed to explain how schemes emerge over stages in development. Operators are meant to be processes that achieve different functions important for scheme development. For instance, the *C* operator is involved in content learning; the *A* operator is involved in affective boosting and inhibition. These operators are combined by the child to move forward in schema development, although exactly how this integration is achieved is not spelled out in detail.

In terms of developmental neuroscience, Arsalidou presents a table that maps constructive operators onto brain regions. In some ways, this is a bit like what happens in cognitive neuroscience: researchers specify a series of cognitive operations or processes thought to underlie behaviour, and then those operations or processes are assigned to different brain regions. In cognitive neuroscience, this is typically based on results from, for instance, functional brain imaging studies (Corbetta & Shulman, 2002). It is not clear what the basis for the mapping to brain regions is here.

Arsalidou gives the reader some sense for how cognitive operations and brain data might come together in Figure 2 with hemispheric dominance hypothesis. The author highlights how this hypothesis differs from the more traditional view of attributing verbal-analytic processing to the left hemisphere and visuospatial processing to the right hemisphere (Heilman & Abell, 1980; Shucard et al., 1977). Instead, Arsalidou points to task demands and mental attention capacity to explain left or right hemisphere dominance from a process-based perspective. The right hemisphere is thought to foster use of automatized processing in overly challenging or easy tasks, while the left hemisphere is thought to be engaged during scenarios requiring effortful working memory, as long as task demands remain equal to the individual's mental attention capacity. For example, Arsalidou suggests when task demands require higher mental attention than an individual's available capacity, the right hemisphere is activated to engage overlearned schemes. This is also the case for low (easy) task demands where automatized processes can do the work. When task demands and mental attentional capacity are relatively equal, the left hemisphere takes the lead. Arsalidou cites some evidence consistent with these proposals.

In terms of our key questions, the theoretical focus in this chapter is on a neo-Piagetian perspective on how schemas change. For instance, Arsalidou focuses on the M-operator later in the chapter, describing how mental capacity grows from infancy through childhood and adolescence, adding one unit of capacity every two years. This growth happens amidst qualitative changes in cognition as children move from, for instance, the sensori-motor stage to the symbolic stage. Exactly how capacity changes is not specified, however. In terms of cognitive neuroscience methods, the chapter describes efforts to use cognitive neuroscience methods like fMRI to test aspects of the theory. Although there is some effort here to map cognitive operators onto brain regions, this mapping and the use of cognitive neuroscience findings seems rather speculative. Thus, in terms of our third question, the integration of neo-Piagetian theory and neuroscience methods here seems to be in its infancy.

Does the cognitive neuroscience of attention offer insights in the development of attention? The chapter by Rueda offers a cognitive neuroscience perspective. Here, developmental theory comes directly from research on the cognitive neuroscience of attention in adults. Figure 2 summarises the adult view, with attention divided into 3 types, although we note a bit of variation in the presentation here. Sometimes, the 3 types are alerting, orienting, and executive; sometimes, the 3 types are activation, selection, and executive. Regardless of the classification, these 3 systems are mapped onto brain regions early in the chapter. The second big theme of the chapter is on the continuum from exogenously driven attention (attention driven from the outside) to endogenously driven attention (attention driven from the inside).

In terms of development, the view here is one of maturation. Rueda describes how attention matures from early activation to later selection to even later executive control over attention. Similarly, she describes movement from more exogenous control over attentional orienting in infancy to more endogenous control later in development as, for instance, children can flexibly switch what they attend to in dimensional card sorting games.

As an example, Rueda begins her survey of early attentional development focusing on sustained attention and infants' progression of interest from simple geometric figures to more dynamic and complex video clips. Early attentional control is discussed as exogenous with saliency and caregiver interaction being pegged as important factors in infant orienting. Nevertheless, early forms of executive attention are evident in the first year including some endogenous regulation of orienting attention. This can be seen in the Gap-Overlap task which highlights how voluntary control of attention is influenced by disengagement. From 1 to 4 months of age, infants show a substantial decrease in the time taken to disengage to a central stimulus, and the delay in orientating to a peripheral stimulus decreases further following this. This reorientation to a stimulus is associated with activation in the frontal region.

Next, Rueda discusses structural changes in white matter across the second year of life. Myelination at this age leads to an enhancement of neural connectivity at this same time we are seeing cohesion amongst diverse executive attention measures. For instance, young children show improvements in the Dimension Card-Sorting Task between 3 and 5 years, which has been associated with refinements in prefrontal networks. Rueda concludes that the maturation of attention and the resulting age-related gains in behaviour are related to changes in both structural and functional connectivity.

In summary, there is a clear perspective in this chapter coming from our understanding of the cognitive neuroscience of attention. Less clear is exactly how movement from early forms of attention to later forms of attention happens. The chapter repeatedly mentions the 'maturation' of brain regions, citing data that connectivity changes and that there are important changes in brain myelination as well. But exactly which mechanisms are responsible for these developmental changes are left unspecified. This means that the chapter presents a concrete theoretical perspective, lots of examples of rich quantitative data using brain imaging methods, and a clear global trajectory for the development of attention. Nevertheless, there is only a loose integration of theory and data here if one wants to understand the mechanisms that drive developmental changes in attention.

The development of the self-concept and a detailed back-and-forth between theory and data. The Crone and van Drunen chapter is a strong example of one way to use neuroscience tools to advance developmental theory. The starting point for this chapter is a verbal theory of how children and adolescents construct a concept of the self. Harter's theory describes two important transitions in how children and adolescents evaluate themselves. Early on, young children have over-positive view of themselves. Later, there is stronger sensitivity to peers and a more realistic self-view. Adolescents also move from a general self-concept to multiple domain-specific selves.

The theory here is broad and relatively descriptive, but this sets the stage for a cognitive neuroscience perspective to explore *how* these changes take place. Here, the authors illustrate what cognitive neuroscience can contribute by peeking under the hood to uncover the processes that underlie social decision-making and self-concept, and by testing proposals about the factors that influence the broad changes over development captured by Harter's theory.

As an example, Crone and van Drunen discuss a "social brain" network involving mPFC, TPJ, precuneus, and STS, highlighting how overlap in these areas with the default mode network may support processes involving the self and others. The default mode network is linked to self-referential thought and self-related processing. In addition, the mPFC is consistently identified as an active region during self-appraisal, regardless of whether this evaluation is from one's own or another's perspective and particularly for positive evaluations. Importantly, the precuneus is also associated with self-concept evaluation and may be acting as a bridge between the default mode network and the typically anticorrelated cognitive control network. Referring to Harter's theoretical framework, Crone and van Drunen discuss the involvement of selective activation in alternative brain regions alongside mPFC and precuneus activation across different domains of self-concept evaluation. For example, when evaluating academic traits in adolescence, the precuneus shows activation. However, when evaluating physical domain traits, there is activation within the anterior cingulate cortex and the dorsolateral prefrontal cortex. Here, we see that areas of activation during physical trait domain evaluation overlap with areas involved with cognitive control, whereas areas involved with academic domain evaluation remain close to the default mode network. Crone and van Drunen discuss the importance of identifying these neural networks to allow for the development of models of self-processing and self-concept understanding.

The authors also use data from structural brain development. Results reveal that variations in structural development of the 'social and self' brain are not exclusively derived from genetic factors. Rather, the developmental period between childhood and adolescence appears to be a critical time window during which individuals are particularly susceptible to the social environment and social experiences. Addition findings from an intervention study looking at experiences during a gap year also support this view, with different functional outcomes for adolescents in the intervention relative to controls.

In summary, this chapter does a nice job of showing an interplay between theory and methods. The authors start with a broad theoretical description of the development of self-concept. They then use sophisticated neuroscience methods to unpack the processes underlie decision-making about the self. In addition, using a twin design, they are able to unpack broad constraints on change over development, showing both genetic contributions to change as well as a critical window for social experiences. Exactly how everything works together will require more work, but this is a strong chapter showing how cognitive neuroscience can contribute to developmental theory.

Neural process models provide a path forward. This special issue presents four chapters with very different perspectives on the integration of theory and cognitive neuroscience methods. In some ways, this diversity is a good thing. It shows that theory and neuroscience methods have been applied in different ways, in different topic areas, with diverse ways to tackle a fundamentally challenging topic: how the brain gives rise to behaviour and how changes in the brain emerge over the timescale of development. The diverse approaches described here suggest there are many ways to tackle this challenging topic. The hope is that this scientific diversity will ultimately prove fruitful as we discover which approaches yield greater understanding.

Diversity can also be a limiting thing as well as it suggests we haven’t quite figured out how to deeply integrate theoretical approaches with neuroscience methods. In this context, we note that one concrete thing missing from this special issue are examples of work using neural process models to advance both theory and methods in our science. For instance, we have been pioneering methods using the framework of Dynamic Field Theory (Schöner et al., 2016) that integrate the concepts of dynamic systems theory together with methods to generate specific predictions about development and test these predictions using cognitive neuroscience methods. We illustrate what such an approach can bring to the study of development with a few concrete examples below.

Dynamic field models are a class of models that approach brain dynamics using the concept of neural population dynamics. That is, the goal is to understand how neural populations in the brain give rise to the brain patterns that underlie human cognition. DFT is fundamentally grounded in an embodied perspective in resonance with many of the arguments put forth by Marshall in his chapter. In particular, we have grappled with the issue of how cognition is grounded both in the spatial and temporal properties of sensory systems as well as the constraints needed to guide actions in context by an organism (Schöner et al., 2016). We have demonstrated that DFT provides a grounded, embodied framework by, for instance, using dynamic field models in a robotics setting, showing how DF models can receive real-time input from camera sensors and guide the activity of effectors to, for instance, allow a robot to make decisions about which object to pick up in simple and complex language tasks (Lomp et al., 2016; Richter et al., 2021).

The goal of DFT is to build an integrated theory of the mind and to understand how that architecture might emerge in development. We have made more progress on the former front, building large-scale architectures recently that handle many aspects of cognition including attention (Grieben et al., 2020), working memory (Johnson et al., 2009; Johnson & Spencer, 2016), scene representations and spatial language (Richter et al., 2021), and even complex language processing with embedded nested noun phrases (Sabinasz &

Schöner, 2023). All of this work demonstrates a commitment to embodiment and grounding higher-level cognition in lower-level sensori-motor systems. In this sense, DFT represents a concrete example of a neuro-cognitive system in full resonance with the embodied brain described by Marshall. We also show concrete ways in which attention can be realised by a neural system, with detailed behavioural modelling of adult attention performance. In this sense, DFT provides a concrete way to formalise some of the ideas from the Rueda chapter as well.

But what about development? Here, DFT is still in its infancy. While we have modelled many aspects of behavioural development, there are still many open questions. For instance, in one body of work we captured developmental changes in visual exploration and visual habituation using a model of autonomous learning (Perone & Spencer, 2012, 2013, 2014). Here, the system changed itself by generalising its own experience – by repeatedly learning about and consolidating colours in working memory, the system boosted its own self-excitatory connections. This led to an increase in the model's working memory capacity, and faster processing of colours over time. This revealed a mechanism for how the system could increase its own working memory capacity, providing a potential mechanism for some of the changes in capacity described by Arsalidou (Simmering, 2016; Spencer, 2020).

We are currently investigating other types of change over development as well. For instance, in recent work on word learning, we have shown how changes in the time scale of longer-term memory dynamics can capture developmental changes in cross-situational word learning tasks (Bhat et al., 2021). Exactly which neural mechanisms might be involved in these changes are still under investigation. But our DF models provide a way to understand how changes in long-term memory processes alter how children and adults organise their behaviours in specific tasks.

A final advance in the use of DFT also speaks to the integration of theory and cognitive neuroscience methods. In recent work, we have shown how DF models can be used to make direct hemodynamic predictions that can be measured using fMRI and fNIRS (Buss et al., 2021). The idea here is to measure how neural activity changes from millisecond to millisecond in the model, and then turn these activation patterns into hemodynamic profiles using methods from the neuroscience literature. This allows us to use a single, integrated model to simultaneously predict measured patterns of brain activity along with behavioural data. We have used this approach to understand the brain dynamics underlying visual working memory in adults. Here we showed that our dynamic field model captured data more effectively than standard analytic methods, shedding light on not just which brain regions were active, but also the function of those brain regions. For instance, results showed that a change detection function in the dynamic field model was best captured by the neural dynamics within the intra-parietal sulcus, a brain region commonly associated with visual working memory capacity (Todd & Marois, 2004). We are still refining these methods, but the promise here is that dynamic field models will not just explain which brain areas are active, but it will also specify the functions in operation in particular brain areas – that is, how patterns of brain activity give rise to particular cognitive operations which ultimately yield behavioural responses.

We have also used this approach to make predictions about how brain activity should change as children's executive function abilities improve between the ages of 3 to 5 years (Buss & Spencer, 2018). Prior work suggested a maturational view with the frontal cortex maturing by 5 years of age to support executive function abilities. Using a dynamic field model, however, we tested a contrasting view that, rather than being immature, the frontal cortex can be driven in a bottom-up way when children engage in supportive executive function tasks. To test this, we simulated a dynamic field model is ‘easy’ and ‘hard’ versions of a dimensional change card sort task. The model predicted that in ‘easy’ task conditions, 3-year-olds would succeed in the card sorting task and would also show frontal engagement driven by bottom-up input from posterior cortical areas. By contrast, in the ‘hard’ version of the task, 3-year-olds would show the canonical pattern of weak frontal engagement. Critically, the model also predicted a modulation of posterior cortical activity with 4-year-olds, with stronger posterior cortical activity in the ‘easy’ task. Results showed the predicted patterns of brain activity measured using fNIRS. Thus, by using a neural process model we were able to make detailed developmental predictions, contrasting a maturational perspective with an experience-dependent perspective where excitatory and inhibitory strengths increase over development (see also, Perone & Spencer, 2013).

In summary, we contend that neural process models provide an excellent way forward to keep theory at the forefront of developmental neuroscience. As a concrete example, dynamic field theory provides a framework where we can create an artificial brain, ensure that this brain can be embedded in a body to interface with the spatio-temporal details of sensori-motor systems, and understand how neural population dynamics give rise to behavioural responses. Furthermore, recent methods show how one can use these models to generate predictions about patterns of brain activity that can be measured with EEG (Spencer et al., 2012), fMRI (Buss et al., 2021), and fNIRS (Buss & Spencer, 2018). Critically, this approach also enables researchers to generate novel developmental hypotheses about the mechanisms underlying change over time. Thus, dynamic field models can provide a critical bridge between brain and behaviour in a way that is directly open to empirical methods as well. We note that DFT is just one approach to understanding how brain and behavioural dynamics co-evolve over time. Other modelling approaches have also yielded novel insights into developmental change (e.g., Lake et al., 2017; Mareschal & Thomas, 2007; McMurray et al., 2012; Westermann & Mareschal, 2004). More generally, then, we think neural process models are an excellent way to integrate theory and cognitive neuroscience methods to understand how change emerges over the timescale of development.

Statements

Conflict of Interest Statement

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Author Contributions

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