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Modeling developmental cognitive neuroscience

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In the past few years connectionist models have greatly contributed to formulating theories of cognitive development. Some of these models follow the approach of developmental cognitive neuroscience in exploring interactions between brain development and cognitive development by integrating structural change into learning. We describe two classes of these models. The first focuses on experience-dependent structural elaboration within a brain region by adding or deleting units and connections during learning. The second models the gradual integration of different brain areas based on combinations of experience-dependent and maturational factors. These models provide new theories of the mechanisms of cognitive change in various domains and they offer an integrated framework to study normal and abnormal development, and normal and impaired adult processing.

Introduction

Brain development is increasingly recognized as playing an important role in cognitive development. Both the experience-dependent elaboration of neural structures within a brain region and the integration of different brain networks have been argued to be closely linked to observed developmental change in diverse modalities such as vision [1], memory [2], face processing [3], and language [4]. This evidence has driven the new field of developmental cognitive neuroscience [5–7] that explicitly aims to relate brain and cognitive development and sees cognitive development as a trajectory emerging from intrinsic and environmental constraints [8,9]. An important insight from this research is that interactions between brain and behavioral development are bidirectional: specific neural structures facilitate certain types of learning, and learning shapes structures of the developing brain [10–12]. Together with theoretical findings that learning in structurally changing systems is fundamentally different from learning in structurally static systems [13], this evidence suggests that to ignore structural development in the brain is to ignore a fundamental mechanism underlying cognitive development.

These insights have also been reflected in computational models of development. Connectionist models have in recent years become the tools of choice for developing and testing precise theories of the mechanisms underlying cognitive development [14–16]. Although most such models consist of a static architecture in which cognitive change occurs through adjusting the strengths of connection weights, other models have explored the role of brain development in cognitive change by integrating structural changes into learning. Here we review the progress and potential of connectionist models within a framework we call Connectionist Developmental Cognitive Neuroscience (CDCN) – models of cognitive development that make explicit reference to brain development by integrating structural adaptation into learning. In addition to exploring developmental constraints from biological predispositions and the environment as in static models, models in the CDCN approach explore of the role of small and large-scale brain changes in cognitive development (Figure 1).

Taking brain development seriously in models of cognitive development

Interactions between brain development and cognitive development operate on different levels. On a small scale, within a cortical region, neural connections are shaped by neural activity (see Box 1). This mechanism allows for localized adaptation of a neural system to specific experiences. On a larger scale, developing projections between different brain areas lead to their gradual functional integration. This process relies on interactions between activity-dependent and maturational processes [17]. CDCN models have addressed each of these aspects of brain development.

Modeling within-region, experience-dependent brain development

Small scale experience-dependent neural development and its interactions with cognitive development have been modeled in constructivist (also termed 'constructive' or 'generative') CDCN models that add or remove units and connections during learning [18–20] (Figure 2). There

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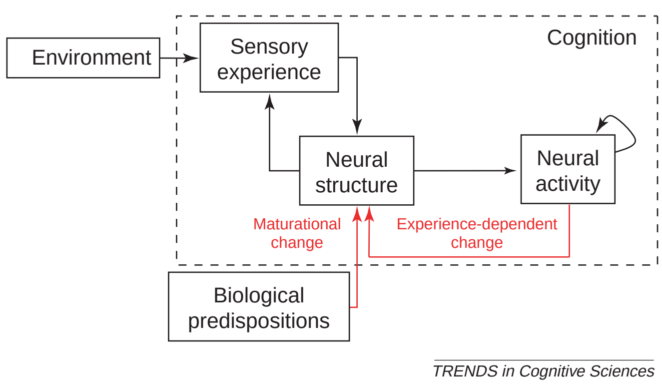

Figure 1. Cognitive development in the CDCN framework emerging from multiple interacting constraints. Biological predispositions constrain the maturation of neural structures in the brain. Neural activity is caused by sensory experience and by previous neural activity. Sensory experience is constrained both by the environment (stimuli) and the neural processing structures. Cognition in this framework is construed as a function of sensory systems, brain circuits, and neural activity. Aspects specific to the CDCN framework are symbolized by the red arrows: maturation as well as neural activity can change neural structure which in turn changes how sensory information is processed. This adaptation leads to different neural activity even under constant sensory input, enabling the building of more complex representations and leading to progressive cognitive development.

are a variety of constructivist neural algorithms [21,22] (see Box 2 for details on three algorithms), but they share many common principles. Most models start with a minimal architecture and are trained on a task until learning no longer improves. At this point a structural adaptation is made by inserting new units and connections. Some algorithms also involve the pruning of units and connections that do not contribute to learning a task. Individual units in a connectionist model are generally not seen as corresponding to individual neurons in the brain, and likewise in constructivist models structural change is not seen as corresponding to the neurogenesis or synaptogenesis of individual neurons. Instead, these models explore the effects of experience-dependent structural change on a more abstracted level. The link to

Box 1. Brain and cognitive development

The interactions between brain and cognitive development have recently become the focus of attention in the new field of Developmental Cognitive Neuroscience [5–7]. Neural activity has long been recognized to play a role in the development of neural structures (for recent overviews see [55,56]). Whereas initially it was believed that this process was dominated by the activity-dependent loss or stabilization of neural connections (neural selectionism [57,58]), more recently the directed growth of neural structures has been suggested as an equally important mechanism (neural constructivism [10,11,55]). Furthermore, recent evidence indicates that, in contrast to a long-held belief, new neurons are generated in different areas of the brain, for example, in the hippocampus (see [59] for an overview). The rate of neurogenesis and survival of the generated neurons is influenced by learning and the complexity of the environment. This research has been supplemented with demonstrations of a surprising functional plasticity of the human cortex (see [60] for an overview). Additional evidence that neural activity mediated by experience has an instructive rather than merely permissive role for the construction of neural structures and connection patterns [61] supports the argument that, together with intrinsic factors and interactions between different brain areas, experience-dependent elaboration of neural structures is a fundamental constraint on cognitive development [17].

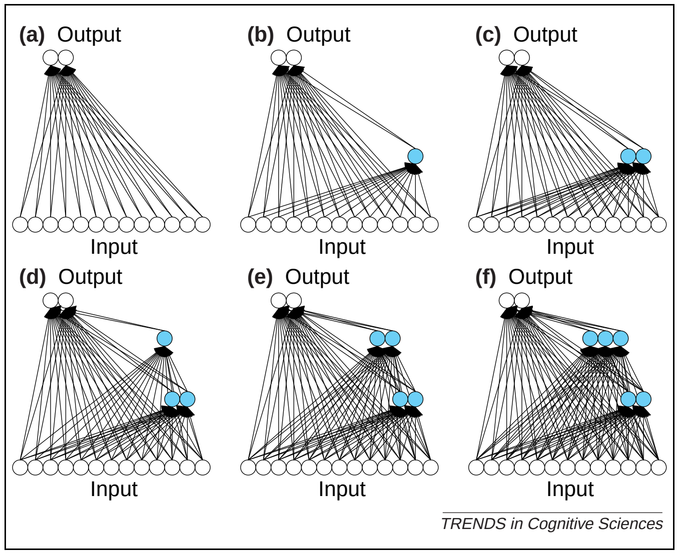

Figure 2. The structural developmental process of a constructivist SDCC network (see also Box 2) modeling the acquisition of conservation of quantity when two rows of objects are presented with varying distances between the objects. The model started with 13 input units describing two rows of objects in terms of length and density, and 2 output units encoding comparison of the number objects in each row **(a)**. During adaptation two hidden layers were recruited with two and three units, respectively, one unit at a time **(b–f)**. This model captured a series of well-replicated psychological regularities (acquisition, sudden spurt, problem-size effect, length bias), whereas a variety of static networks failed to learn the training patterns [25,68].

brain development exists because both in the brain and in constructivist models, adaptation leads to a network structure that depends on specific aspects of the learning task such as the frequency of patterns and the difficulty of the mapping from inputs to outputs (Figure 2). By using

Box 2. Constructivist algorithms

One constructivist model that has been used extensively in modeling psychological development is the Cascade-Correlation (CC) algorithm [32] and its variant, Sibling Descendant Cascade Correlation (SDCC) [62]. Like most constructivist algorithms, a CC model learns in a static architecture until the error can be reduced no further and then recruits a new unit. Recruitment occurs as randomly-initialized weights from all input units to each of typically eight candidate recruits are adjusted with the goal of maximizing the correlation between candidate-unit activation and existing network error. The candidate unit with the largest absolute correlation is then installed into the network in a new or existing layer [62]. The algorithm then continues to learn by adjusting weights from the input and hidden units to the output units until the error again stagnates. Figure 2 shows the emerging topology of a network that learned about conservation of quantity [25].

A different constructivist algorithm used in modeling cognitive development is Supervised Growing Neural Gas (SGNG) [20,63]. In SGNG, inserted hidden units have Gaussian activation functions and respond to inputs falling into their receptive fields. The size of a unit's receptive field is determined by its distance to neighboring units. Each hidden unit has an error counter to measure its contribution to the overall output error. Inserting a new unit is done by splitting the existing hidden unit with the highest accumulated error in two. This leads to a covering of the input space with receptive fields at varying densities, reflecting the experience-dependent adaptation to the learning task.

Another class of constructivist networks [64] combines evolution and development by evolving the specific ways in which experience can affect axonal growth and synaptogenesis. In these models neural positions and instructions for neural growth evolve over several generations, but axonal outgrowth itself is triggered by neural activity. In this way interactions between genotypic and phenotypic development can be studied.

constructivist neural networks for modeling cognitive development the significance of experience-dependent neural development for cognitive change can then be studied.

Why model structural change?

Two important questions for CDCN models are whether their learning is different from static models, and whether integrating structural change adds any new insights into the mechanisms of cognitive development [13,23]. To answer these questions, static and constructivist models have been directly compared on several well known developmental phenomena.

Comparing constructivist and static models

Two main results of comparisons between static and constructivist models have been that constructivist models can often better capture the developmental trajectory observed in children than static models, and that they are often more successful in reaching adult competence.

Balance scale

One example is the balance-scale task [24]. In this task children view a rigid beam with weights on each side at particular distances to the fulcrum. The children then have to predict which side of the beam will drop. Children's performance on this task progresses through four distinct stages which differ in the types of problems the children can solve [24]. In modeling this developmental trajectory, both static and constructivist models progressed through the first three of these four stages, but only constructivist networks settled in a stable final stage of correct performance [25].

Integrating time, velocity and distance

Other comparisons were made between models of the integration of velocity, time, and distance cues for moving objects. In these tasks, children are given information on two of these dimensions (e.g. time and distance) and then have to predict the third (e.g. velocity). Between 5 and 10 years children progress through developmental stages characterized by different rules for making inferences about the missing dimension. Constructivist networks were able to capture these stages accurately [26], but it proved impossible to simulate the same process in static models. Static networks with too few hidden units failed to reach the final stages, but increasing the size of the hidden layer by a single unit resulted in a model that missed intermediate stages [27].

Learning the English past tense

Another example of model comparisons is the acquisition of the English past tense. The main challenge in this domain is to account for children's characteristic error patterns with overregularizations of irregular verbs (such as *goed* and *eated*) before all forms are learned. Static models of this process have not normally been able to learn all irregular forms even after extensive training, and they sometimes rely on changes in the training data to mimic children's error patterns [28–30]. These problems were not encountered by a constructivist model [31] that reached adult competence, and in which gradual structural development led to an internal reorganization of representations resulting in error patterns comparable to those observed in children even when the language environment was held static.

Together, these models indicate that structural change is responsible for stage-wise behavioral change in the modeled domains. In addition, structural change often allows the model to learn all of the task when it could not previously do so, providing a mechanism for the transition from development to adult competence.

Why do constructivist models work?

The main reason for the success of constructivist models in accounting for developmental stages is that structure is inserted gradually and in response to a model's experience with the learning task. Constructivist models start with a minimal architecture that forces them to initially focus on the broad aspects of a task. Units that are inserted can then directly focus on more specific, unsolved aspects of the task. By contrast, in fixed architectures all units initially try to solve the main part of the learning task because each unit aims to reduce the global error independently from the others. This 'herd effect' has been shown to dramatically slow down learning in static compared with constructivist models [32]. Such initial dedication of all units to the same part of a problem can make it difficult to cover all aspects of the task as learning progresses, resulting in failure to reach adult competence. Further, in contrast to maturational models where change proceeds independently from learning [33], constructivist models use experience by inserting structure only as the task requires, resulting in an architecture that reflects the statistical properties of the task. Modeling in constructivist networks therefore provides insights into how experiences impact on the brain's processing structures, for example in the development of modularization and regions of specialization [19,20,25].

The ability of these models to account for developmental trajectories and resulting adult level competence supports the view that experience-dependent structural change within a brain region supporting a particular task is an important aspect of development of this task in infants and children.

Modeling inter-regional brain development

Whereas constructivist networks focus on experience-dependent brain development within a cortical region, other CDCN models have examined the gradual integration between different brain regions and its functional consequences. These models build on evidence for multiple interacting (cortical and subcortical) brain systems with different functional specializations, for example in adult memory [34] and vision [35]. CDCN models have explored the emergence of such interactions and their behavioral consequences in infants.

Visual development

One example is a model of visual processing in which a dorsal pathway is specialized on spatial-temporal processing and a ventral route on invariant object features [36,37]. In this model, one component implemented the dorsal route with an algorithm that learned to process spatial-temporal information, while the other component implemented the ventral route with a competitive algorithm that learned spatially invariant feature representations. Outputs from both components were integrated in a system modeling an infant's response to a visual stimulus. Based on this experience-dependent integration, the model accounted for the developmental lag between infants' knowledge of hidden objects and their ability to demonstrate this knowledge in a retrieval task in terms of the added computational demands of integrating separate neural systems in the retrieval task [37].

Habituation

A similar approach was taken in a model of habituation based on one subsystem implementing inhibition in a hippocampal module and another implementing potentiation in a cortical module [38,39]. Gradual maturation of the connections between these two subsystems led to cross-talk between them and modeled the developing habituation behavior of infants, including an age dependent shift from a preference for familiar items to one for novel items.

Speech development

Two other models accounted for the development of vowel repertories in infants based on a developing integration between articulatory gestures and their resulting speech sounds [40,41]. These models suggested that a gradually developing link between auditory and motor cortical areas based on babbling leads to perceptual and production prototypes in the infant. The models further implemented mechanisms by which experience with an ambient language biases the perceptual and production systems towards that language.

Gaze following

In another model, development of gaze following was simulated in a robot equipped with a neural network control system that learned to generate motor commands based on visual and haptic information [42]. This model reproduced the developmental stages found in the gaze following of infants. Other models of gaze following used reinforcement and temporal difference learning methods to explain infants' developing executive control through strengthening interactions between basal ganglia and frontal cortex [43].

In addressing behavioral development across a variety of domains, these models have suggested precise mechanisms for developing interactions between brain regions and their effects on psychological processing. In most of the models, the behavior of younger infants is explained as relying on one of the specialized brain systems in isolation. Gradual integration with another system then leads to representational change, resulting in behavioral change and the development of more complex behaviors such as reaching for objects, gaze following, and imitation of sounds from an ambient language. In this way, these models explain developmental trajectories as a direct consequence of structural integration, lending further support for the CDCN framework that emphasizes the role of structural change in cognitive development.

Challenges to the CDCN approach

Despite the success of CDCN models in accounting for developmental phenomena some authors have argued that they are not valid models of development. Raijmakers and colleagues [44] believe that developmental transitions should not be explained by discontinuous changes to the learning system such as structural growth. However, this view is in contrast to evidence for experience-dependent development in the brain (see Box 1) where synaptogenesis and neurogenesis constitute qualitative changes to the learning system. Another criticism [45] maintains that constructivist models do not construct new representations but merely proceed from testing simple to complex pre-existing hypotheses as they develop. However, this view is contradicted by theoretical analyses indicating that structural growth of a learning system leads to an increase in its representational complexity [13,23].

Regulating growth

Nevertheless, the CDCN approach raises some important questions. Structural change in the brain is not arbitrary or uniform but depends on interacting genetic and environmental factors. Excessive or reduced neural growth in certain brain areas has been linked to developmental disorders such as autism [46]. These findings underscore the importance of understanding the mechanisms by which neural development is regulated and suggest that structural development in CDCN models needs to be constrained. One way of achieving this constraint is by combining mechanisms for structural elaboration with mechanisms for loss of units and connections [47]. Another approach is based on a 'wave of plasticity' sweeping the cortex and enabling neural adaptation only in the area of its peak [48]. Yet there have so far been few principled investigations of these issues in relation to cognitive modeling, and more research is clearly needed to better understand the interactions between weight adaptation, structural growth and data coverage in constructivist models. Furthermore, as our understanding of experience-dependent development in the brain increases, new biologically inspired constraints, concerning for example interactions between experience-dependent and maturational factors and the timescales of neural growth and pruning, should be integrated into CDCN models.

Explaining critical periods

A further challenge for CDCN models concerns developmental phenomena explained in static models where the absence of structural change is a core assumption of the explanation. An example is critical periods of plasticity in learning and development. Recent theories suggest that timing and duration of critical periods in some domains might depend on learning in a fixed architecture leading to entrenchment of representations [49,50]. An understanding of how precisely previously learned and new knowledge interact in CDCN models will require more principled investigations and further comparisons between static and CDCN models of cognitive development.

The promise of CDCN models

Despite these open questions, CDCN models provide, through linking structural and cognitive change, precise and testable new explanations for developmental change in a wide variety of domains. This work serves to narrow somewhat the large gap in understanding relations between brain and cognitive development.

Development and adult processing

In addition to successfully accounting for cognitive change, the CDCN framework suggests a tightly integrated view of cognitive development and adult processing. This is because in the CDCN framework the developing system is viewed as shaped by interactions between intrinsic factors and experience, and the adult system is an outcome of this developmental process. From this perspective, understanding of both normal and impaired adult processing benefits from being analyzed through a developmental lens, asking which constraints lead to the observed final state and what this tells us about the nature of this final state [16,51]. For example, whereas cognitive neuropsychology often explains selective impairment in adults after brain injury by invoking encapsulated modules, the CDCN approach views the functional specialization of cortical regions as emerging from interactions between an environment and mechanisms of experience-dependent structural development. This 'Neuroconstructivist' perspective has also been applied to characterizing developmental disorders [52,53], and CDCN models provide a useful tool for specifying how variations in early constraints can lead to abnormal developmental trajectories and an abnormal adult state [54]. In this way, CDCN models can potentially integrate normal and abnormal development with normal and impaired adult processing within a unified explanatory framework.

Conclusions

In this review we have outlined the CDCN approach to the connectionist modeling of psychological development. The main force of models in this approach comes from linking brain development and cognitive development by integrating structural change into their adaptation mechanisms. These models address structural change both within brain regions in the form of experience-dependent insertion and removal of units and connections, and the integration between different (cortical and subcortical) regions based on interactions between maturational and experience-dependent factors. The CDCN approach complements Developmental Cognitive Neuroscience by providing implemented models in which cognitive development can be studied as emerging from interactions between intrinsic and environmental constraints with adult cognitive processing as its end state (Figure 1). Biological predispositions are reflected in initial network structures, an adaptation algorithm, and attention to and interpretation of specific aspects of the environment. Environmental effects can be modeled by variations in the data on which a model is trained. Finally, constraints imposed by brain development can in the CDCN framework be studied through the structural development of the computational system during learning.

Box 3. Questions for future research

- Can models be developed that in a single system successfully account for normal and abnormal development and normal and impaired adult processing in a specific cognitive domain?
- How can developmental models be successfully used to address the question of rehabilitation after brain injury?
- When different models account for the same data, how can they be compared? Can a common framework be developed in which to characterize different static and CDCN models?
- Some models account for brain development not by structural change but by changes in learning parameters such as learning rate, steepness of the activation curve, gradually reducing noise or changing receptive field sizes (e.g. [65–67]). How do these changes relate to structural change in a network and in the brain?

More principled research needs to be done and many questions remain to be answered (see Box 3), but we believe that in linking structural and functional development, CDCN models have the promise of providing a unified framework for studying normal and abnormal cognitive development and normal and impaired adult cognitive processing.

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