

Processes of change in brain and cognitive development

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We review recent advances in the understanding of the mechanisms of change that underlie cognitive development. We begin by describing error-driven, self-organizing and constructivist learning systems. These powerful mechanisms can be constrained by intrinsic factors, other brain systems and/or the physical and social environment of the developing child. The results of constrained learning are representations that themselves are transformed during development. One type of transformation involves the increasing specialization and localization of representations, resulting in a neurocognitive system with more dissociated streams of processing with complementary computational functions. In human development, integration between such streams of processing might occur through the mediation of language.

Introduction

There is general agreement among contemporary researchers that developmental psychology needs to move away from static descriptions of the cognitive system at different ages, and instead strengthen its focus on the underlying mechanisms that generate change [1]. Recent advances, some of which are described in other articles in this issue, have opened potential new avenues for examining mechanisms of change. However, as yet there has been no systematic attempt to review the ways in which evidence from neuroimaging, neural-network modeling, cognitive studies and atypical development can converge to reveal these processes. In this article our goal is to review and assess current advances in understanding the processes of cognitive developmental change. Two important advances in this endeavor are research on learning mechanisms that drive developmental change, and research on the types of representational change that occur in development. We begin with a focus on learning mechanisms, discussing a range of proposed developmental learning mechanisms, the constraints that operate on such mechanisms, how these mechanisms relate to one another, and the potential of such mechanisms to account for developmental change. We then focus on representational change, discussing a range of proposed representational changes, the mechanisms that lead to these representational changes, how these representational

changes relate to one another, and the potential of such representational changes to account for developmental change. We conclude with a thumbnail sketch of how different processes of learning, constraints, integration and dissociation might combine to generate human cognitive development.

Learning mechanisms

Several types of learning mechanisms may drive developmental change. These include self-organizing, error-driven, statistical and constructivist learning. These are not mutually exclusive learning mechanisms but they have been studied separately to some degree.

Learning mechanisms have often been studied within the neural-network modeling framework, where learning mechanisms can be specified in working simulations and their effects can be tested. Within the neural-network framework, two broad classes of learning mechanisms have been delineated [2]: self-organizing learning and error-driven learning. As suggested by their names, these types of learning differ in the forces that guide them. Error-driven learning is guided by the goal of reducing errors, measured as a function of the difference between target states and actual states. Such targets can be manifest in various ways, such as a teacher explicitly correcting a child's behavior, the environment providing a target signal for an infant's expectations about what they will see next, and an infant's goal of reaching to a particular location providing a target signal for the attempted motor action. Backpropagation [3] is one of the most common variants of error-driven learning algorithms, and has been applied to understanding several developmental phenomena [4–6].

However, in some cases learning occurs in the absence of any apparent errors [7,8] or without the abundance of target signals required in some error-driven learning simulations. Self-organizing learning mechanisms may be at work in such cases. Rather than being driven by an overall goal of reducing errors, self-organizing learning entails a process of forming representations that capture important aspects of the environmental structure. When these aspects of the environment are relevant to task performance, such self-organizing representations may also be useful in reducing errors, but they are not shaped with any constraints from how they affect task performance. Rather, self-organizing learning occurs based on patterns of simultaneous activation among processing

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units. Hebbian learning algorithms [9], whereby ‘units that fire together, wire together’, are one of the most common forms of self-organizing learning algorithms, and have been applied to understanding several developmental phenomena [10,11].

Learning and sensitive periods

Both error-driven and self-organizing simulations have been used to investigate why there are sensitive periods in development, when learning is most effective. For example, error-driven models have provided a very different perspective on why learning a second language is more difficult later in life [12]. These models show how learning can lead to neurobiological changes that reduce plasticity, rather than plasticity changing according to a purely maturational timetable. The key computational insight from such models is that, before a system develops expertise, it is highly plastic, with connections readily changed in response to error signals. As the system learns through such changes in connections, the system becomes much less sensitive to error signals; the system becomes ‘entrenched’. From this perspective, a second language is harder to learn later in life because of the learning of the first language that has occurred. The interference from the first language is exacerbated by the fact that attempts to learn a second language are usually interleaved with continued use of the first language. Two languages can be learned more easily early in life because neither has become entrenched while the other is being learned. In this manner, sensitive periods might arise because early learning reduces later learning [12].

In other cases, the learning that occurs after sensitive periods may be counterproductive. A self-organizing model was used to demonstrate how this process could lead to sensitive periods in phoneme discrimination, where attempts to learn new information lead to the strengthening of incorrect responses [13]. For example, each time monolingual Japanese speakers hear English /r/ and /l/ sounds, they might strengthen the associations between those distinct inputs and a representation of the single Japanese phoneme that is a blend of the English sounds. This learning would be counterproductive, strengthening the tendency to hear the distinct English sounds as the single Japanese sound. Consistent with this account, infants who could initially discriminate two speech sounds failed to discriminate them after repeated presentation of the sounds in the context of a unimodal distribution of sounds [14]. Learning from such experience led to the representation of a single sound, as in the case of the Japanese blend of English /r/ and /l/ sounds.

Statistical and constructivist learning

Another approach to learning focuses on infants’ remarkable abilities to extract statistical regularities in the environment, from relatively brief exposures to auditory or visual stimuli (e.g. [15,16]). Recent work within this statistical learning approach has demonstrated the importance of variability in the environment for learning [17] (Box 1). To date, neural-network explorations of infant statistical learning have tended to be error-driven (e.g. [18–20]). However, learning of statistical regularities

Box 1. The importance of variability for learning

Variability aids infants’ learning of non-adjacent statistical dependencies, in which statistical regularities span intervening information [17]. In one experiment, infants were presented with one of two artificial languages with three-element strings: language A strings were of the form aXb and cXd, and language B strings were of the form aXd and cXb. The languages contained the same adjacent dependencies (a and X, X and b, etc.) but could be distinguished by their non-adjacent dependencies (e.g. a and b versus a and d). The size of the pool from which the X elements were drawn was varied; infants learned the non-adjacent dependencies when the set size was 24, but not when it was 12 or 3. Such variability also aids infants’ category-based abstractions, which may be relevant to their learning of categories such as function words (the, a, etc.). This work might therefore ultimately address fundamental debates such as those concerning language learnability [17].

can occur through both self-organizing (e.g. [2,21]) and error-driving learning algorithms [22].

Finally, many learning mechanisms have been explored within a constructivist approach [23], in which learners actively contribute to the construction of their knowledge rather than being passive recipients of information. One kind of learning mechanism within this framework allows models to shape the information they receive based on how they behave; for example, with models’ eye-gaze actions affecting the information they see and, in turn, what they learn [24]. This kind of system contrasts with standard models, which receive a set sequence of input patterns regardless of how they behave. Another kind of learning mechanism that has been explored within this framework allows models to grow during the process of learning, through the recruitment of new units as a function of the errors the models make [25]. Such models have been applied to several Piagetian tasks, and raise interesting possibilities concerning a potential correspondence between stage-like cognitive developments and the recruitment of new units. These models may also highlight the importance of the developmental process. Models show different profiles of behavior if they recruit units dynamically as they learn rather than simply starting with the final number of units in a static network.

Given that there are several powerful learning mechanisms that could be involved in development, it becomes relevant to investigate how these mechanisms are constrained such that they learn about stimuli or events that are of adaptive relevance to the developing child.

Constraints on learning

In this section we discuss the types of constraints that operate on learning processes in development. Learning is not infinitely flexible or general during development; instead, constraints seem to govern what can be learned and when. For example, early in development, learning can be highly stimulus specific, such that children exhibit learning only when the testing context very closely matches that of the learning context. In addition, learning in some domains seems to be guided by constraints relevant to stimuli in those domains. Constraints on learning apply across a variety of domains: object processing, face processing, social cognition, memory and word learning.

The first type of constraint that merits discussion comprises constraints imposed by the intrinsic specificity of the learning system itself. For example, Hayne [26] has reviewed evidence from preverbal infants performing learning tasks such as ‘mobile conjugate reinforcement’ and concluded that these experiments support an ‘encoding specificity hypothesis’ originally advanced by Tulving and Thompson [27]. This hypothesis states that a stimulus can serve as an effective retrieval cue if, and only if, that stimulus had been part of the original encoding. For example, in the mobile conjugate reinforcement paradigm infants learn to move their foot to move an attractive mobile hanging overhead. However, even if only small changes are made to the mobile (such as changing more than one object out of five within the mobile), infants no longer seem to associate their leg kick with the mobile movement.

Intrinsic constraints have also been argued to operate early in development for object and word learning. With regard to object recognition, Baillargeon and colleagues [28] have explored the proposal that infants’ learning about objects is constrained by the principle of continuity [29]. The principle states that objects exist and move continuously in time and space, and this might constrain how visual scenes are parsed by infants (and adults) [29]. Recent experiments by Baillargeon and team have revealed that infants sometimes also track the physical properties of objects as they move in time and space. For example, if infants represent the height of an object that is placed inside a container or under a cover (because previous contextual manipulations induced them to do so), then they expect the object to retain its height as the event unfolds and they are surprised if it does not [28]. Similarly, in word learning several theorists have argued that internal lexical constraints bias infants to favor certain inferences or hypotheses when determining the meaning of a new word. For example, if a child is shown an object and told to ‘Look at the blicket’, they are likely to assume that ‘blicket’ denotes the whole object rather than a part or property (e.g. Markman’s ‘whole object constraint’ [30]). However, recent studies by Markson [31] suggest that the learning mechanisms underlying the acquisition of words might be more general, and that the ‘special’ features of this form of learning might derive instead from rapid learning about the relevant information about objects, and from the ability of infants to reason about the intentions of others. The special role of others (parents or caregivers) in constraining what and how infants and children learn has led some to propose that there is a human-specific ability, ‘pedagogy’, that relates to our inclination to transmit relevant information to each other [32]. According to this theory, pedagogy is a teacher-guided learning process whereby arbitrary associations (such as putting names to objects) can be formed quickly and effectively. The view is that human infants are biased to learn from infant-directed teaching and are sensitive to the cues that indicate teaching contexts, such as gaze direction and pointing. Some have suggested that this bias to attend to other humans is present from birth, although whether the underlying mechanisms for this

bias are specific to the configuration of a face remains controversial [33].

A complementary approach to investigating mechanisms of change in cognitive development is to focus on the transformations that occur in mental and neural representations, and it is to this topic that we now turn.

Representational change

Although there is much controversy about the appropriate definition of ‘representation’, we use the term in its most general sense to refer to patterns of activation within the brain that correspond to aspects of the external environment. We will consider what we have learned about changes in representations from the perspective of behavioral, modeling and neuroimaging work, with typical and special populations.

Studies in developmental cognitive neuroscience across several domains are beginning to give insights into how representations change during postnatal development. For example, behavioral and electrophysiological studies of face processing in infants and children have led to the hypothesis that this processing becomes increasingly specialized, or finely tuned, during development. Event-related potential results show that a unique signature of processing human upright faces does not emerge until after 6 months; before that age the ERP correlates of processing upright and inverted faces are exactly the same [34]. Corresponding behavioral results have led some to postulate mechanisms of ‘perceptual narrowing’ [35] or ‘increased specialization’ [36]. Related to this type of change may be a corresponding decrease in the extent of brain activation in response to faces [37,38]. The importance of experience early in development for such processes has been demonstrated through studies of cataract-reversal patients, who show some lasting deficits in face processing despite removal of cataracts within the first few months of life [39].

If functional specialization of systems within the typical brain is at least partly a result of postnatal development, this will have implications for our view on developmental disorders [40]. Specifically, one way to explore how uneven cognitive profiles result from neurogenetic developmental disorders is to assess the effects of varying the different parameters that constrain learning within neural networks [41]. Changes in certain parameters before learning takes place can disrupt the typical patterns of functional specialization that emerge within such networks. For example, slightly changed competition parameters within the network tended to disrupt specialization and result in poorer task performance in some domains, but not others. The perspective afforded by such models challenges the notion that developmental disorders result from patterns of sparing and impairment in innate cognitive modules for language, face processing, and so on. Instead, the developmental process is viewed as crucial for understanding the nature of the representations that emerge to support such functions.

Another perspective on representational change is driven by the view of children as active scientists, developing intuitive theories of the world around them. Specifically, an important aspect of children’s developing

representations may be their 'causal maps' of the world, which constitute abstract, coherent, learned representations of the causal relationships between events [42]. When presented with a 'blicket detector' that lights up and plays music when 'blickets' are placed on it, children draw fairly complex causal conclusions about which objects are blickets and which are not. For example, if two objects together are shown to make the blicket detector go, and then one of the objects alone is shown to make the blicket detector go, children are much less likely to refer to the other object as a blicket. This kind of causal learning and inference is argued to be consistent with the Bayes net formalism, which provides a normative account of how causal structure can be inferred from patterns of evidence [42].

The wide variety of representational changes considered here has advanced understanding of cognitive developmental change across many domains, and provides important constraints and challenges for theories and models of development. However, one important class of transformation, that of integration and dissociation, remains to be discussed.

Dissociation and integration

This section explores two, apparently opposing, proposals about the transformation of information during development. One view is that perceptual and cognitive development involves the increasing integration of streams of information, and the other view is that development involves increasing segregation or dissociation of processing streams. The notion that development involves the increasing segregation of streams of information originally comes from work in neuroscience, and thus potentially provides another example of how information on brain development can shape our thinking about cognition. The 'pruning' of synapses, fiber bundles and sometimes cell bodies is a prominent feature of postnatal brain development in primates (and other mammals) [43]. This pruning is often said to be selective in that it reduces connectivity between specific regions, pathways or 'blobs' within the cortex resulting in 'parcellation' [44]. Some theorists have speculated that this aspect of brain development will have consequences for perceptual and cognitive development. In particular, younger children and infants may show behavioral hallmarks of combining streams of information that are kept distinct in adults [45,46]. For example, adults are very poor at direction of motion judgments when red/green color stimuli are involved because motion pathways in cortical processing (magnocellular pathway) are generally separate from color-sensitive pathways (parvocellular pathway). In adults, brain pathways that encode direction of object motion generally do not also process color [47]. This dissociation of processing means that in psychophysical experiments adults are very poor at detecting the direction of motion (as measured by directionally appropriate eye movements) of red and green striped colored gratings (see Figure 1). By contrast, infants of 2–4 months old were much better than adults at detection, suggesting that color input to motion processing is relatively stronger in the immature

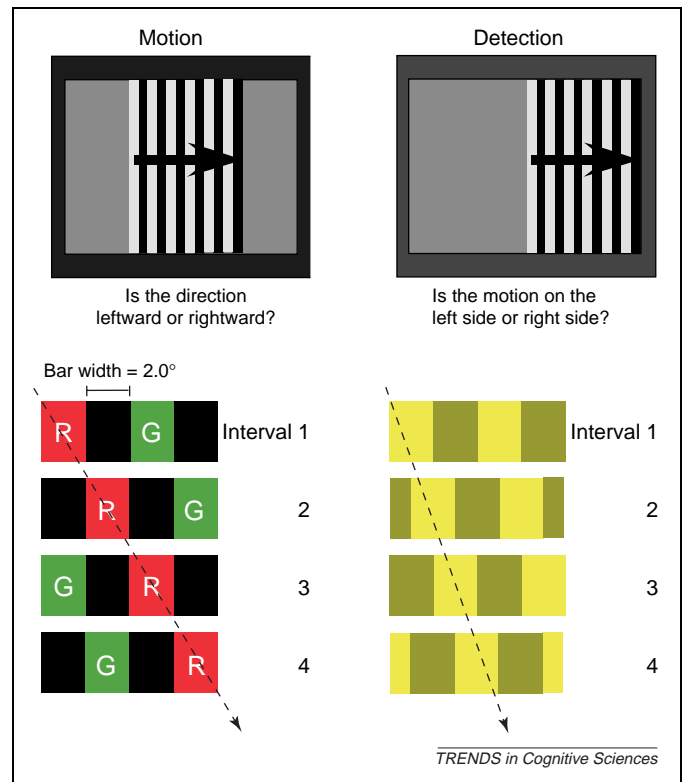


Figure 1. Examples of the stimuli used to show an increasing dissociation between color and motion processing during development. Adults are poor at making judgments of direction of motion when matched red and green stripes are used. By contrast, infants are able to use color information to detect direction of motion; however, performance reduces as they get older. This reveals a process of increasing segregation of these streams of information with age [48].

visual system. Furthermore, younger infants showed more evidence of this integration than did older children, demonstrating a dynamic process of increasing segregation of these streams of information [48].

A more general argument about increasing dissociation during development has been mounted by Daphne Maurer, who has suggested parallels between the processing of sensory information by infants and those of adult synesthetes [45]. Synesthesia is a condition in which adults have specific merging of information from different senses, such as an association between a color and a sound. Maurer points to several lines of evidence that young infants also merge information from different senses in this way. In one line of evidence, newborns seem to show forms of cross-modal matching not seen at older ages. However, unlike the specific matching on information from different sensory modalities seen in adults and older children, in newborns the matching is coarse and might simply reflect the 'energy' in the stimulus rather than its specific content [45].

Processes of increasing integration

Whereas the evidence discussed above indicates that the dissociation of systems occurs during perceptual and cognitive development, it can be argued that a process of increasing integration characterizes other aspects of development. For example, the failure of infants to encode both the location and surface features of a hidden object has been attributed to a lack of integration between the

dorsal and ventral visual pathways. A specific computational model has been advanced to account for the development of infants' perception and encoding of objects that assumes a process of increasing integration of information about location (dorsal pathway) and surface features (ventral pathway) [49].

Moving from perception to cognition, Carey has proposed that several changes in numerical cognition during development can be attributed to the increased integration between previously independent systems [50]. Carey's idea is that children construct a true concept of number and gain arithmetic skills by bringing together their two initial systems of number representation, and that language plays a central role in integrating these independent systems (see **Box 2**).

Evidence that we have reviewed from perceptual and cognitive development suggests that both processes of integration and dissociation occur during development. Viewed from the perspective of the brain this should be no surprise because, although there is overall 'pruning' of synaptic contacts, this reflects general changes in an overall population of synapses that is changing continually. As suggested recently by O'Reilly [51], different brain

systems evolve and develop with different, but complementary, computational trade-offs. For example, learning in the hippocampus is different from that in the cortex with respect to learning rate and level of overlap between activation patterns. Similarly, the dorsal and ventral visual pathways discussed earlier may develop increasingly divergent specialization, with one extracting and encoding information about the location and graspability of objects and the other encoding surface features relevant for visual recognition [49]. This 'divide and conquer' strategy might initially be the most efficient way to develop brain functions, but after some time there is a need to integrate across these divergent computational routes, and so processes of integration become necessary. One proposal is that increasing patterns of dissociation during development reflect the process of specialization of different neural structures and pathways so that they reduce redundancy and generate pathways with different computational trade-offs. However, once complementary, rather than duplicative, computational routes have been achieved, then mechanisms for overall integration are required. 'Whole brain' models, such as those advanced by O'Reilly and colleagues [51], or models of competition and cooperation between pathways will help to illuminate these developmental changes.

Box 2. Integration and numerical cognitive development

Evidence from comparative, developmental and adult functional imaging studies suggests that there are at least two independent number-related systems in the human brain [52,53]. The first system is an 'analog-magnitude' representation, and is thought to represent quantity by a representation that reflects physical magnitude proportional to the items being enumerated. In such a system, 'numerical' comparisons are made in a similar way to length or time comparisons. The second system is involved in representing the exact numerosity of very small sets of objects [54]. Some have suggested that this system is an 'object-file' system that evolved originally to allow us to track up to about four moving objects at a time [55]. Although both of the above systems are number domain relevant, they are not domain specific in that they can be engaged by non-numerical tasks. Behavioral studies of human infants provide evidence that both these systems exist in humans and emerge early in development [55]. When children attend school and learn elementary arithmetic, however, they must work with a different system of number representation: a system that does not have an upper limit, that is not constrained by the Weber fraction, that is not constrained by perception, and that can be related to language including number words. This system has been termed an 'integer-list' representation [50]. How do human children construct this system?

One idea is that children construct a new concept of number and gain arithmetic skills by bringing together their two initial systems of number representation, and that language – the number words and the verbal counting routine – plays a central role in orchestrating these systems [50]. One of several lines of evidence that support this view is that when children learn the number words and the counting routine, they first map 'one' to the object-file system and all other number words to the analog-magnitude system indiscriminately: for example, they respond correctly when they are presented with arrays of one and of four objects and are asked to point to the array with 'one' versus 'four', but they respond at chance when presented with arrays of two versus four or eight objects and asked to point to the array with 'two' versus 'four' or 'eight' [55]. Next, children coordinate the systems together to learn the meanings of 'two' and 'three', but continue to use all other number words indiscriminately to mean (roughly) 'some'. Finally, children surmise that each word in the count sequence refers to an array that includes one more entity, and a larger overall set size, than the array picked out by the previous word in the count sequence [55].

Conclusion

We have reviewed many recent advances in the study of processes of change in brain and cognitive development, through research on learning mechanisms and investigations of representational changes (see **Figure 2**). These advances span a range of domains, methods and populations. Although many questions remain (see **Box 3**), we are encouraged that this recent body of work reveals important principles that may now be extended to other domains. The key points we consider to be important are that the developing brain incorporates powerful error-driven and self-organizing learning mechanisms that are heavily constrained by intrinsic factors (some mechanisms are better at acquiring particular types of information), other brain systems (such as subcortical biases), and interactions with the physical (e.g. objects, space) and social ('pedagogy') environment. During development, the

Box 3. Questions for future research

- Does one type of learning mechanism best account for changes during cognitive development, or do we need to invoke different varieties of learning for different problems?
- Are constraints on learning during development more commonly imposed by intrinsic factors, or by the nature or quality of interaction with human caregivers?
- To what extent can information about the mechanisms of developmental change in the brain inform our thinking about changes at the cognitive level?
- What are the relationships between the various types of proposed representational changes during development (e.g. perceptual narrowing, causal map formation, emergent effects in developmental disorders), which are often investigated at different levels and through different methodologies?
- How do we reconcile evidence for increasing integration of systems during development with evidence for increasing dissociations between systems?

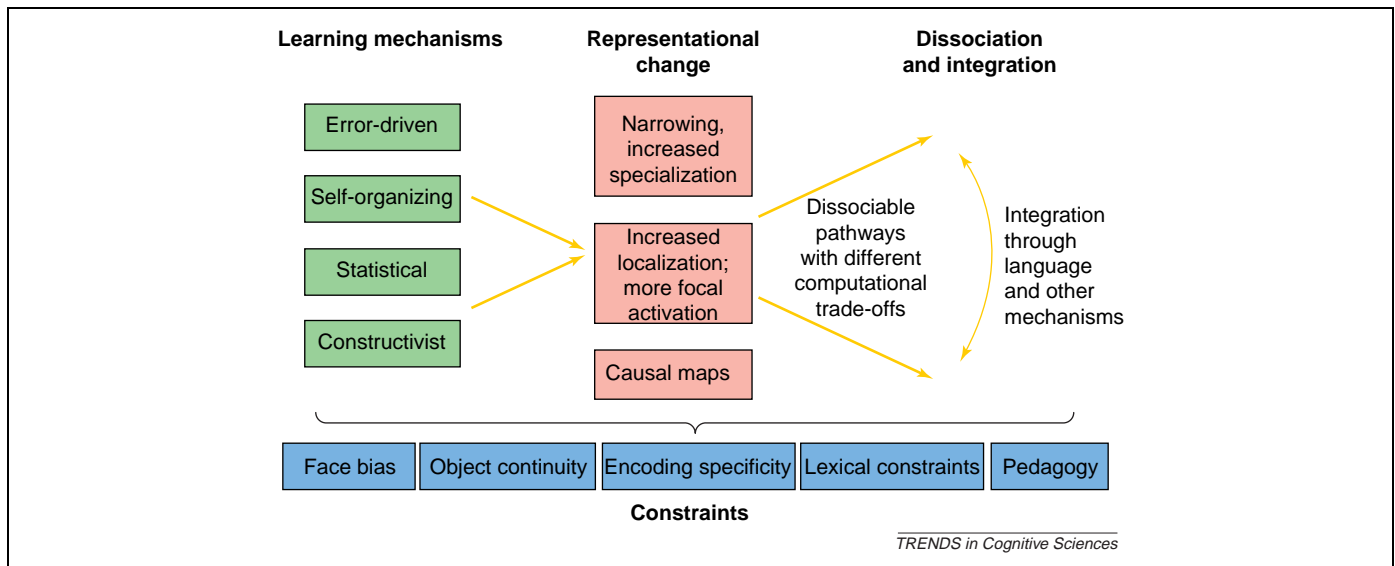


Figure 2. A summary diagram illustrating possible relationships between mechanisms of developmental change. The diagram is not intended to indicate information flow during processing, or a developmental sequence, but only to illustrate possible links.

representations that emerge as a product of these powerful but constrained learning mechanisms become increasingly specialized and localizable within the brain. We suggest that this general process can result in increasing dissociation between systems as they adopt a 'divide and conquer' approach to information processing. With increasing dissociation between streams of processing, the need for structured integration increases, and in humans language might play a role in this.

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