CHAPTER

# 11

# Theories in Developmental Cognitive Neuroscience

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## 11.1 INTRODUCTION

Recently a new field of science has emerged at the interface between developmental neuroscience and developmental psychology. This field has come to be known as developmental cognitive neuroscience (DCN) (Johnson, 2010). The exciting mix of these previously separate fields has led to a burgeoning of new observations, methods, and ideas. However, a characteristic shared with most newly emerging interdisciplinary areas in the biological sciences is the feeling that the knowledge acquired to date is rather fragmentary, with many intuitively surprising observations remaining unexplained. How can one understand these phenomena, and interpret and explain them within a broader context of other findings with different methods and populations? To do this, one needs to develop theories, and, the author will argue that these theories need to be of a particular kind to be useful.

As a scientific discipline, DCN sits at the convergence of two of the oldest philosophical and scientific debates of mankind. The first of these questions concerns the relation between mind and body, and specifically between the physical substrate of the brain and the mental processes it supports. This issue is fundamental to the scientific discipline of cognitive neuroscience. The second debate concerns the origin of organized biological structures, such as the highly complex structure of the adult human brain. This issue is fundamental to the study of development. Light can be shed on these two fundamental issues by tackling them both simultaneously, and specifically by focusing on the relation between the postnatal development of the human brain and the cognitive processes it supports.

The second of the two debates above, that of the origins of organized biological structure, can be posed in terms of phylogeny or ontogeny. The phylogenetic

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(evolutionary) version of this question concerns the origin of the characteristics of species, and has been addressed by Charles Darwin and many others since. The ontogenetic version of this question concerns individual development within a life span. The ontogeny question has been somewhat neglected relative to phylogeny since some influential scientists have held the view that once a particular set of genes has been selected by evolution, ontogeny is simply a process of executing the instructions coded for by those genes. By this view, the ontogenetic question essentially reduces to phylogeny (a position sometimes termed 'nativism'). In contrast to this view, many now agree that ontogenetic development is an active process through which biological structure is constructed afresh in each individual by means of complex and variable interactions between genes and their environments. The information is not in the genes, but emerges from the constructive interaction between genes and their environment (see also Oyama, 2000).

What actually is ontogenetic development? Many introductory biology textbooks define development in terms of an increasing restriction of fate. This refers to the basic observation that as the biological development of an individual organism (ontogeny) proceeds, the range of options for further specification or specialization available to the organism at that stage decreases. Structural or functional specialization is an end state in which there are few or no options left to the organism. By this view, plasticity can be defined as a developmental stage in which there are still options available for alternative developmental pathways (Thomas and Johnson, 2008). Another dimension of ontogenetic development is that it involves the construction of increasingly complex hierarchical levels of biological organization, including the brain and the cognitive processes it supports. As is seen later in this chapter, organizational processes at one level, such as cellular interactions, can establish new emergent functions at a higher level, such as that associated with overall brain structure. This characteristic of ontogeny means that a full picture of developmental change requires different levels of analysis to be investigated simultaneously. The author argues that the developmentalist needs to go beyond statements such as a psychological change being due to maturation, and actually provide an account of the processes causing the change at cellular and molecular levels. Thus, in contrast to most other areas of psychology and cognitive science, a complete account of developmental change specifically requires an interdisciplinary approach.

Given the above considerations, it is perhaps surprising that only recently has there been renewed interest in examining relations between brain and cognitive development. Although the field of developmental psychology was originally founded by biologists (such as Darwin and Piaget), biological approaches to human behavioral development fell out of favor in the 1970s and 1980s for a variety of reasons, including the widely held belief among cognitive psychologists in that period that the software of the mind is best studied without reference to the hardware of the brain (see section 11.2 for the details of this argument). However, the recent explosion of basic knowledge on mammalian brain development makes the task of relating brain to behavioral changes considerably more viable than previously. In parallel, molecular and cellular methods, along with theories of self-organizing dynamic networks, have led to great advances in our understanding of how vertebrate brains are constructed during ontogeny. These advances, along with those in noninvasive structural and functional neuroimaging, have led to the recent emergence of DCN.

## 11.2 WHY DO WE NEED THEORIES?

Some might argue that, as a subfield of biology, investigators in DCN should proceed with their empirical investigations of human development unbiased by any perspective or theory, or simply wait until enough data are in before speculating on its significance. However, even a cursory read of philosophy of science tells you that this view is, at best, somewhat naïve. While Victorian naturalists simply made observations about the animals and plants they studied, when one moves to a modern science led by experiments, the rules change. The experiments choosen to conduct (out of the many millions of potential experiments that could be done) are inevitably guided by implicit assumptions and biases. For example, many of the earliest functional MRI experiments with children professed to be neutral and exploratory while also assuming that new brain regions becoming on-line with increased development would be seen. As will be seen later, in many cases this basic starting assumption was violated. In addition, theories in science do not just attempt to explain sets of data *post hoc*, but they should actually generate predictions and direct whole lines of empirical investigation.

Having emphasized the importance of theories, we must also be sure to achieve an appropriate balance with data gathered from a variety of different sources and methods. In one of the parent disciplines of DCN, cognitive development, several grand theoretical castles have been built on the shaky sands of just one particular type of behavioral test. In most of the biological sciences, confidence in an observation or conclusion is greatly increased by seeking multiple different sources of converging evidence.

Interdisciplinary fields such as DCN face a formidable challenge in the development of adequate theories since scientists are required to develop theories that not only cross different levels of observation (such as genetic,

neural, and behavioral), but also relate those different levels together in some way. Ideally, DCN theories should relate evidence from different levels of observation in terms of one level of explanation. As mentioned earlier, for several decades in the field of cognitive development, it was generally considered inappropriate to attempt to relate different levels of explanation. Rather, the aim was to explain one level of observation (change in behavior) in terms of one level of explanation (cognitive). This widespread view was taken for a variety of reasons, but one influential source was the work of Marr (1982). Marr argued that because the same computation can, in principle, be implemented on different computer or neural architectures, a computational account of cognition could, and should, be constructed independently of the details of its implementation on hardware. This influential argument led to the view that considering the role of the brain in cognitive development was reductionist in the sense that molecular and cellular processes could never provide an adequate explanation of cognitive processes.

While the case against a simple reductionist view is clearly correct, as stated earlier, theories of biological development critically need to explain the reverse process (to reductionism) of the emergence of higher-order structures of organization. Thus, while not denying Marr's anti-reductionist point, constructing a specific type of neural computer hardware will constrain the range of possible computations that could be supported. With these considerations in mind, Mareschal et al. (2007), among others, argue that there are constraints on computation imposed by its detailed implementation. Further, when attempting to bridge levels of explanation, mechanistic accounts of processes of computation and developmental change should be consistent across different levels, that is, there is a need for isomorphism between levels of description. Since the goal of DCN is to relate the genetic, neural, cognitive, and behavioral accounts of human development, devising theories that relate the different levels of observation seems crucial. Mareschal et al. (2007, p. 209) thus describe it "We would argue that strong pragmatic considerations mean that what is achievable in real time at one level of description strongly constrains the appropriate theories of what is going on at other levels. What is more easily achievable in the brain will strongly constrain the character of cognition. More specifically, the brain can implement much more readily certain representational states and transformations more than others. It is these primitives that the researcher should initially use to construct theories of cognition."

Theories come in different shapes and sizes. Specifically, the amount and range of DCN data accounted for can independently vary along at least two dimensions: (a) how domain specific or domain general (domain here is used in a general sense to refer to an aspect of cognition) a theory is, and (b) how many levels of explanation are incorporated or integrated. It is a defining feature of DCN, as opposed to traditional cognitive development, that multiple levels of observation are considered and related in terms of a single process or causal mechanism. One reason for this is that the parent discipline of cognitive development had been built on the strategy of explaining changes in behavior during development in terms of cognition – a level of explanation that is not itself directly observable. While the scientific strategy of theorizing at a level that is not directly observable is not unique to cognitive psychology, constraining theories of this kind by only one level of observation is of high risk because of the lack of constraints it imposes. In other words, a very wide variety of theories can successfully account for data at one level of observable only. It is proposed that a better strategy is to sandwich a nonobservable level of explanation (such as cognition) between two levels of observable, such as those of brain and behavior.

Theories in DCN could potentially vary enormously in the scope of data that they account for, from a single cognitive domain in a single population to an account that crosses domains of cognition and populations (typical and atypical development). Often, in biology, the broader the scope of a theory, the less clearly it makes detailed domain-specific predictions. Thus, some have referred to such broad-scope theories as frameworks (Kuhn, 1996). Put simply, frameworks are ways of thinking about, or viewpoints on, a large body of data. Frameworks may have some testable elements but primarily serve as a coherent set of assumptions that, taken together, offer an account of a wide range of phenomena. In addition, within a framework, more specific and detailed theories (and thence hypotheses) can be constructed. Further, they guide lines of research and the kinds of hypotheses that are explored. In a young and newly emerged field, it is suggested that the first priority should be to develop appropriate and useful frameworks, since adopting the wrong framework could be an expensive diversion in terms of both time and money.

## 11.3 THREE FRAMEWORKS FOR UNDERSTANDING HUMAN FUNCTIONAL BRAIN DEVELOPMENT

A review of the literature reveals that three different frameworks on human postnatal functional brain development are currently commonly adopted and explored (Johnson, 2001).

### 11.3.1 Maturational Viewpoint

According to the maturational viewpoint, newly emerging sensory, motor, and cognitive functions are related to the maturation of particular areas of the brain,

usually regions of cerebral cortex. Much of the research to date attempting to relate brain to behavioral development in humans has taken this approach. Evidence concerning the differential neuroanatomical development of brain regions should then predict the age when a particular region is likely to become functional. Conversely, success in a new behavioral task at given age is attributed to the maturation of a new brain region. Functional brain development is, in this sense, depicted as the reverse of adult neuropsychological studies of patients with brain damage, with specific brain regions being added-in during development (with the converse effects from being depleted by damage).

Despite the intuitive appeal and attractive simplicity of the maturational approach, it does not successfully explain many observations on human functional brain development. For example, recent evidence (discussed later) suggests that some of the regions that are slowest to develop by neuroanatomical criteria can be activated shortly after birth and appear to mediate cognitive functions even before they would be considered anatomically mature. Thus, the emergence of new behaviors is not necessarily linked to a previously immature, silent neural region becoming active when it matures. In fact, where functional activity has been assessed by fMRI during a behavioral transition, multiple cortical and subcortical areas appear to change their response pattern (e.g., Luna et al., 2001; Supekar et al., 2009) rather than a few specific areas becoming active. Another difficulty for the maturational viewpoint is that associations between neural and cognitive changes based on age of onset are theoretically weak because of the great variety of neuroanatomical and neurochemical measures that change at different times in different regions of the brain. Thus, as the brain is continuously developing until the teenage years, it is nearly always possible to find a potential neural correlate for any behavioral change in development.

### 11.3.2 Interactive Specialization

In contrast to the maturational viewpoint, the interactive specialization (IS) viewpoint assumes that postnatal functional brain development, at least within cerebral cortex, involves a process of organizing patterns of interregional interactions (Johnson, 2000, 2001, 2010). According to this view, the response properties of a specific cortical region are partly determined by its patterns of connectivity to other regions, and their patterns of activity. During postnatal development, changes in the response properties of cortical regions occur as they interact and compete with each other to acquire their role in new computational abilities. From this perspective, some cortical regions may begin with poorly defined broad functions, and consequently are partially activated in a wide range of different stimuli and task contexts. During development, activity-dependent interactions between regions sharpen the functions and response properties of cortical regions such that their activity becomes restricted to a narrower set of circumstances (e.g., a region originally activated by a wide variety of visual objects may come to confine its response to upright human faces). The onset of new behavioral competencies during infancy will, therefore, be associated with changes in activity over several regions, and not just by the onset of activity in one or more additional region(s).

### 11.3.3 Skill Learning

The third perspective on human functional brain development, skill learning, involves the proposal that the brain regions active in infants during the onset of new perceptual or motor abilities are similar, or even identical, to those involved in complex skill acquisition in adults. For example, Gauthier and colleagues have shown that extensive training of adults to identify individual artificial objects (called greebles) eventually results in activation of a cortical region previously preferentially activated by faces, the fusiform face area (Gauthier et al., 1999). This indicates that this region is normally activated by faces in adults, not because it is prespecified to do so, but because of our extensive expertise with that class of stimulus. Extended to development, this view would argue that development of face processing during infancy and childhood could proceed in a similar manner to acquisition of perceptual expertise for a novel visual category in adults (see Gauthier and Nelson, 2001). While the degree to which parallels can be drawn between adult expertise and infant development remains unclear, to the extent that the skill-learning hypothesis is correct it presents a clear view of a continuity of mechanisms throughout the life span.

## 11.4 ASSUMPTIONS UNDERLYING THE THREE FRAMEWORKS

Underlying these frameworks are differing sets of key assumptions.

### 11.4.1 Deterministic Versus Probabilistic Epigenesis

Gottlieb (1992) distinguished between two approaches to the study of development; deterministic epigenesis in which it is assumed that there is a unidirectional causal path from genes to structural brain changes and then to psychological function, and probabilistic epigenesis in which interactions between genes, structural brain

changes, and psychological function are viewed as bidirectional, dynamic, and emergent. In many ways, it is a defining feature of the maturational approach that it assumes deterministic epigenesis; region-specific gene expression is assumed to effect changes in intraregional connectivity that, in turn, allows new functions to emerge. A related assumption commonly made within the maturational approach is that there is a one-to-one mapping between brain and cortical regions and particular cognitive functions, such that specific computations come on-line following that maturation of circuitry intrinsic to the corresponding cortical region. In some respect, this view parallels mosaic development at the cellular level in which simple organisms (such as *Caenorhabditis elegans*) are constructed through cell lineages that are largely independent of each other (see Elman et al., 1996 for discussion). Similarly, different cortical regions are assumed to have different maturational timetables, thus enabling new cognitive functions to emerge at different ages.

In contrast to the maturational approach, IS has a number of different underlying assumptions. Specifically, a probabilistic epigenesis assumption is coupled with the view that cognitive functions are the emergent product of interactions between different brain regions. In this respect, IS follows current trends in adult functional neuroimaging. For example, Friston and Price (2001) point out that it may be an error to assume that particular functions can be localized within a certain cortical region. Rather, they suggest that the response properties of a region are determined by its patterns of connectivity to other regions as well as by their current activity states. By this view, "the cortical infrastructure supporting a single function may involve many specialized areas whose union is mediated by the functional integration among them" (p. 276). Similarly, in discussing the design and interpretation of adult functional MRI studies, Carpenter and collaborators have argued that "In contrast to a localist assumption of a one-to-one mapping between cortical regions and cognitive operations, an alternative view is that cognitive task performance is subserved by large-scale cortical networks that consist of spatially separate computational components, each with its own set of relative specializations, that collaborate extensively to accomplish cognitive functions" (Carpenter et al., 2001, p. 360). Extending these ideas to development, the IS approach emphasizes changes in interregional connectivity as opposed to the maturation of intraregional connectivity. While the maturational approach may be analogous to mosaic cellular development, the IS view corresponds to the regulatory development seen in higher organisms, in which cell–cell interactions are critical in determining developmental fate. While mosaic development can be faster than regulatory, the latter has several advantages. Namely, regulatory development is more flexible and better able to respond to damage, and it is more efficient in terms of genetic coding. In regulatory development, genes do not code directly, but need only orchestrate cellular-level interactions to yield more complex structures (see Elman et al., 1996).

### 11.4.2 Static Versus Dynamic Mapping

As well as the mapping between structure and function at one age, it can also be considered how this mapping might change during development. When discussing functional imaging of developmental disorders, Johnson et al. (2002) point out that many laboratories have assumed that the relation between brain structure and cognitive function is unchanging during development. Specifically, in accord with the maturational view, when new structures come on line, the existing (already mature) regions continue to support the same functions they did at earlier developmental stages. The static assumption is partly why it is sometimes considered acceptable to study developmental disorders in adulthood and then extrapolate back in time to early development. Contrary to this view, the IS approach suggests that when a new computation or skill is acquired, there is a reorganization of interactions between different brain structures and regions. This reorganization process could even change how previously acquired cognitive functions are represented in the brain. Thus, the same behavior could be supported by different neural substrates at different ages during development.

Stating that structure–function relations can change with development is all very well, but it lacks the specificity required to make all but the most general predictions. Fortunately, the view that there is competitive specialization of regions during development gives rise to expectations about the types of changes in structure–function relations that should be observed. Specifically, as regions become increasingly selective in their response, properties during development patterns of cortical activation during behavioral tasks may therefore be more extensive than those observed in adults, and involve different patterns of activation. Additionally, within broad constraints, successful behavior in the same tasks can be supported by different patterns of cortical activation in infants and adults. Evidence in support of this view will be discussed later.

The basic assumption underlying the skill-learning approach is that there is a continuity of the circuitry underlying skill acquisition from birth through to adulthood (see Poldrack, 2002; Ungerleider, et al., 2002 for review of the neural systems involved in perceptual and motor skill learning in adults). These circuits are likely to involve a network of structures that retains the same basic function across developmental time

(a static brain–cognition mapping). However, other brain regions may respond to learning with dynamic changes in functionality similar or identical to those hypothesized within the IS framework. For example, neuroimaging studies of adults acquiring the skill of mirror reading show both increases and decreases in cortical activity over widespread regions during learning: unskilled performance is associated with activation in bilateral occipital, parietal, and temporal lobes and cerebellum, with acquisition of skill leading to decreases in bilateral occipital and right parietal activation and to increases in inferior temporal lobe and caudate nucleus activation (Poldrack, 2002). According to the skill-learning view, similar dynamic changes in brain activation would occur as skills emerge during development.

### 11.4.3 Plasticity

Another way in which the three perspectives differ is with regard to the concept of, and assumptions about, plasticity. Plasticity in brain development is a phenomenon that has generated much controversy, with several different conceptions and definitions having been presented. According to the maturational framework, plasticity is a specialized mechanism that is activated following brain injury. According to the IS approach, plasticity is simply the state of having a region's function not yet fully specialized. That is, there is still remaining scope for developing more finely tuned responses. As mentioned earlier, this definition corresponds well with the view of developmental biologists that development involves the increasing restriction of fate. Finally, according to the skill-learning hypothesis view, the functional plasticity present in early development may share many characteristics with the plasticity underlying acquisition and retention of skills in adults (Karni and Bertini, 1997). Thus, unlike the IS approach, plasticity does not necessarily reduce during development.

### 11.4.4 Summary

To summarize, the maturational view is characterized by the interrelated assumptions that (1) cortical areas are a mosaic of regions with independent developmental timetables; (2) deterministic epigenesis means that inherent structural development in a region causes or allows functional changes; (3) there is fixed regional structure/function mapping; and (4) plasticity involves specialized mechanisms triggered by injury. In contrast, the IS approach is based on the assumptions that (1) cortical areas are inextricably linked through dense patterns of interconnections that contribute to coordinated sequences of development; (2) probabilistic epigenesis gives a vital role to intrinsically and extrinsically generated activity in sculpting anatomical development; (3) combinations of cortical regions may support similar or identical behaviors in different ways during the course of development; and (4) plasticity is the inherent state of an unspecialized neural system. The third perspective, skill learning, is based on the assumptions that (1) specific cortical areas or networks are specialized for perceptual and motor skill acquisition from early on; (2) the acquisition of these skills shapes the response functions of the same or other cortical regions; (3) dynamic changes occur in the neural substrate of a skill as the brain becomes expert; and (4) plasticity is retained at fairly constant level throughout development.

## 11.5 PREDICTIONS AND EVIDENCE

Frameworks are useful for a variety of reasons, but particularly so when they help to generate predictions that direct research (albeit that they will not always make opposing predictions), and when they offer coherent explanations of previously puzzling observations. This section presents, three of the sources of evidence that an adequate account of human functional brain development will need to address. Before this, however, the author reviews the types of predictions that arise from the three approaches. The first set of predictions concerns the neural correlates of the onset of new abilities during development. According to a maturational view, new behavioral abilities are mediated by new components of cognition that are, in turn, enabled or allowed by the maturation of one or more brain regions. A consequence of this is a general increase in the number of structures that can be activated in tasks with development. In contrast to these predictions, in the IS approach, it is anticipated that widespread networks of brain regions will change their patterns of activation in association with the onset of new behavioral abilities. Specifically, regions become more specialized (finely tuned) in their response properties with experience. A consequence of this specialization is that on at least some occasions, fewer brain regions will be activated with specific stimulus or task contexts. Turning to the skill-learning approach, here it is anticipated that the onset of new abilities will often be associated with activation of a network of skill acquisition areas. As the new behavioral ability is acquired, a different network of brain regions may become involved.

With regard to the issue of how functions are mapped on to patterns of brain activity, according to the maturational approach, if two age groups are compared in a task for which they show identical behavioral performance, it should also be expected to see identical patterns of brain activation. This is not necessarily the case for the IS approach since the exact patterns of brain

activation that support a function will change according to the degree of specialization of component regions within the supporting network. Indeed, the IS approach predicts that the patterns of regional brain activation supporting a function will change during development. While the exact nature of this change will depend on the degree of specialization achieved in different component structures, the IS view predicts a general trend for a decrease in the extent of cortical activation with increasing development/experience. The skill-learning view invokes the reactivation of one or more skill-learning circuits at the onset of a task, followed by a different pattern of activation after the skill is acquired. In this case, in many comparisons between age groups, the younger group will have acquired the skill in less depth than the older group, giving rise to different patterns of underlying brain activation. Interestingly, however, patterns of changing brain activation while adults acquire new skills should mirror the changes seen during development as infants and children acquire simpler skills.

## 11.6 FUNCTIONAL BRAIN IMAGING

Elsewhere, evidence from functional imaging pertaining to the development of face perception and social cognition (Cohen-Kadosh and Johnson, 2007; Johnson, 2010; Johnson et al., 2009) has been reviewed in detail. In this section, evidence is reviewed from the functional neuroimaging of normal development that pertains to the three perspectives on functional brain development described above. The author suggests that the evidence currently available does not offer much support to the maturational view, at least not without substantial modification. Instead, behavioral change often seems to be accompanied by large-scale dynamic changes in the interactions between regions, and different cortical regions become more specialized for functions as a consequence of development.

A maturational approach to human postnatal functional brain development predicts that a neural correlate of increasing behavioral abilities is an increasing number of active cortical areas. In functional imaging paradigms, therefore, infants and children should show fewer regions active in tasks where they show poorer behavioral performance than adults. In contrast, if new behaviors require changes in interregional interaction, a greater or equal extent of cortical activation can be predicted, and different patterns of activation might be found early in development even in task domains where behavioral performance is similar to that of adults. Which of the three approaches is adopted not only has theoretical implications, but also practical implications for data collection. For example, if one adopts the maturational approach and is expecting a particular area to become active during development for a particular task, then brain imaging may be focused on that region rather than on the whole brain. As a consequence, any possible changes in more distant brain structures would not be detected. By contrast, if one adopts the IS approach, then the importance of whole-brain imaging is clearly apparent.

A number of authors have described developmental changes in the spatial extent of cortical activation in a given situation during postnatal life. Event-related potential experiments with infants have indicated that for both word learning (Neville et al., 1992) and face processing (de Haan et al., 2002), there is increasing localization of processing with age and experience of a stimulus class. That is, electrophysiological recordings reveal a wider area of processing for words or faces in younger infants than in older ones whose processing has become more specialized and localized. From the IS framework, such developmental changes are accounted for in terms of more pathways being partially activated in younger infants before experience with a class of stimuli. With increasing experience, the specialization of one or more of those pathways occurs over time. Taking the example of word recognition, ERP activity differentiating between comprehended and noncomprehended words is initially found over widespread cortical areas. This narrows to left temporal leads after children's vocabularies have reached a certain level, irrespective of maturational age (Mills et al., 1993). Changes in the extent of localization can be viewed as a direct consequence of specialization. Initially, multiple pathways are activated for most stimuli. With increasing experience, fewer pathways become activated by each specific class of stimulus. Pathways become tuned to specific functions and are therefore no longer engaged by the broad range of stimuli, as was the case earlier in development. Additionally, there may be inhibition from pathways that are becoming increasingly specialized for that function. In this sense, then, there is competition between pathways to recruit functions, with the pathway best suited for the function (by virtue of its initial biases) usually winning out.

Further evidence to support the IS view comes from functional MRI studies in children. For example, Luna et al. (2001) tested participants aged 8–30 years in an occulomotor response-suppression task. Their behavioral results showed that the adult level of ability to inhibit prepotent responses developed gradually through childhood and adolescence. The difference between prosaccade and antisaccade conditions was investigated with functional MRI, and revealed changing patterns of brain activation during development. Both children and adolescents had less activation than adults in a few cortical areas (superior frontal eye fields, intraparietal sulcus), and several subcortical areas, a finding broadly consistent with maturational hypotheses. However, both children and adolescents also had differential

activation in regions not found to show differences in adults. Children displayed increased relative activation in the supramarginal gyrus compared to the other age groups, and the adolescents showed greater differential activity in the dorsolateral prefrontal cortex than children or adults. These findings illustrate that the neural basis of behavior can change over developmental time, with different patterns of activation being evident at different ages, a pattern consistent with the IS and the skill-learning viewpoints.

A similar conclusion can be reached after examination of the developmental fMRI data produced by Casey and colleagues. These authors (Casey et al., 1997; Thomas et al., 1999) administered a go/no-go task to assess inhibitory control and frontal lobe function to healthy volunteers from 7 years of age to adult. The task involved participants responding to a number of letters, but withholding their response to a rarely occurring 'X.' More than twice the volume of prefrontal cortex activity (dorsolateral prefrontal cortex) was observed in children compared to adults. One explanation of this finding is that children found the task more difficult and demanding than adults. However, children with error rates similar to those in adults showed some of the largest volumes of prefrontal activity suggesting that task difficulty was not the important factor. It is difficult to account for these decreases in the extent of cortical activation in terms of the progressive maturation of prefrontal cortical areas. The finding that children and adults appeared to show different patterns of activation even when performance was equated is inconsistent with the skill-learning viewpoint, but is in line with expectations from the IS viewpoint.

The third example of the use of fMRI to study the development of cortical activation patterns during childhood comes from studies of verbal fluency tasks in which participants are asked to generate words in response to a cue (e.g., to generate examples of a target category, or generate a verb that relates to a cued noun). Several studies have shown that adults (Lehéricy et al., 2000) and school-age children (Gaillard et al., 2000; Hertz-Pannier et al., 1997, 1999) typically activate left hemisphere frontal cortical networks including Broca's area, premotor, prefrontal, and supplementary motor areas as well as, less consistently, temporal cortical areas including superior temporal, middle temporal, and supramarginal gyri. In addition, some degree of activation in homologous right frontal regions is almost always found both in adults (Pujol et al., 1999; Springer et al., 1999) and in children (Gaillard et al., 2000; Hertz-Pannier et al., 1997, 1999). Two studies have found that both the degree to which activation is bilateral (rather than left dominant) and the extent of this activation is greater in children than in adults (Gaillard et al., 2000; Holland et al., 2001). Thus, as in the other examples discussed above, typical development is associated with a reduction in the extent of activation of cortical areas and, as a consequence, an increased lateralization of activation to the left hemisphere with age (Holland et al., 2001).

In sum, the balance of evidence to date suggests that (1) new behavioral skills are accompanied by widespread changes across many regions of cortex, and (2) functional brain development involves the twin process of increasing localization and increasing specialization.

## 11.7 CRITICAL OR SENSITIVE PERIODS

The three perspectives on human functional brain development differ in their views as to the effects of early atypical experience. By the maturational view, differences in experience might influence the speed at which a function matures or the ultimate level of performance; in the skill-learning view, any atypical early experiences can potentially be compensated for later in development as the mechanisms for learning remain in operation in the same way; in the IS view, atypical early experiences could have long-lasting effects because they could affect the specialization and localization of function, which may not be able to be altered later in life when there is less scope for plasticity.

There have only been a limited number of studies examining the effects of atypical early experience in humans. Some studies have investigated the perception of facial information in children who experienced deprivation of patterned visual input in the early months of life due to bilateral, congenital cataracts. These patients were tested years after their cataracts were removed and they were fitted with contact lenses (i.e., years after visual input had been restored), thus any effects of the few months of deprivation following birth would likely be absent or very minimal according to the maturation or skill-learning views. However, investigation of these patients reveals persistent deficits in selective aspects of face processing. One study found that patients showed impairments in matching facial identity over changes in viewpoint (and tended to show an impairment in recognizing identity over changes in emotional expression), but performed normally on tests of lip-reading, perception of eye gaze, and matching of emotional expressions (Geldart et al., 2002). The second study demonstrated that this difficulty in processing facial identity may be due to deficits in processing the spacing among facial features since patients performed normally in discrimination of faces that differed only on individual features (e.g., mouth) but they were impaired in discrimination of faces that differ only in the spacing of the features (Le Grand et al., 2001). This was not due to a general impairment in perception of spacing of features, as they performed normally in discriminating nonface patterns whether they differed by the shape

of the features or the spacing of the features. The fact that these impairments persisted even after years of visual input to compensate for the early deprivation is not consistent with the maturational or skill-learning views, but is consistent with the IS view that early atypical experience may have long-lasting consequences.

The three perspectives that have been discussed yield different types of predictions about the consequences of perinatal brain damage. According to the maturational view additional mechanisms of plasticity are activated following early damage. Specific additional explanations are then required to account for incidents of recovery of function. In addition, it is not obvious why the extent of plasticity is greater earlier in life. From the IS perspective, there is a parsimonious explanation of recovery of function following perinatal damage since the regional specialization of the remaining brain regions will be altered to compensate, particularly, the corresponding regions in the other hemisphere. In cases of bilateral or extensive damage, recovery is less likely. From the skill-learning perspective, plasticity is a life-long feature of the brain. Damage to the general circuits critical for skill acquisition will have long-lasting and widespread consequences, whereas damage to circuits specific to acquisition of particular skills or their retention may result in more isolated impairments. Of the three approaches, IS gives the simplest account of sensitive periods for plasticity since plasticity is reduced when specialization of corresponding regions is achieved.

In sum, with regard to the long-term effects of atypical early experience, or even variations of experience within the normal range, once again the three frameworks lead to different sets of expectations. From the skill-learning perspective variations in early experience will determine the extent of skills acquired. Early deprivation will be potentially reversible since the same mechanisms of skill acquisition are available later in life. From the IS perspective, long-term effects of atypical early experience can result from atypical patterns of regional specialization arising early in life. Such atypical patterns of specialization may be difficult to reverse once established. Finally, under the maturational view, a primary variable influenced by the environment is the speed of maturation that may affect the level or maintenance of a skill. It is sometimes argued that early sensory deprivation may have a general slowing effect on the sequence of maturation.

## 11.8 ATYPICAL DEVELOPMENT: FROM GENETICS TO BEHAVIOR IN DCN

It has been seen in earlier sections that IS is a promising framework for understanding human functional brain development. While this level of explanation may be appropriate for characterizing the proximal causes of atypical cognition or behavior in developmental disorders such as autism or Williams's syndrome, when development goes awry, a satisfactory explanation of the disorder also requires an account of the causal mechanisms that initiate the atypical development trajectory. This usually entails hypotheses about how an atypicality at one level (such as genetics) causes or induces the onset of atypical development at other levels (brain, cognitive, behavior). An initial attempt to provide a framework for unraveling these complex causal pathways in developmental disorders came with the causal modeling approach of Morton and Frith (1995). According to its originators, causal modeling provided a theory-neutral system for modeling different theories about the paths of causation from a biological level to cognitive and behavioral levels. The models were represented in a graphical notation that allowed for easy comparison between competing explanations, but the framework itself did not involve the construction of computational or neural network models (although a theory represented in the notation could potentially be implemented this way).

Causal modeling is a useful way to compare different theories where these theories are based on the assumption of predetermined epigenesis (a one-way causal pathway from genetics to behavior), but it is a less natural format for capturing the complexities of probabilistic epigenesis (Gottlieb, 2007) in which cause can also run in reverse – for example, sensory experience or internal states such as stress are known to affect gene expression profiles. In addition, causal modeling is intended as a notation for comparing different theories, and as such does not provide an explanation or generate testable hypotheses itself.

A different perspective on identifying causal factors in development involves using implemented computational models that can capture complex nonlinear interactions that are hard to conceptualize with just schematic illustrations or verbal descriptions. Here, the assumption is that multiple factors can interact in complex ways to determine outcome. In one of several initial attempts to apply neural networks to developmental disorders, Oliver and colleagues charted the different ways in which the 'normal' formation of structured representations in the cerebral cortex can go wrong (Oliver et al., 2000). These models were originally designed to investigate the mechanisms underlying the IS process discussed earlier. Several groups have used simple cortical matrix models to investigate the factors and mechanisms responsible for cortical specialization (e.g., Kerszberg et al., 1992; Oliver et al., 2000; Shrager and Johnson, 1995). In these artificial neural networks, connections between nodes are pruned according to variations of Hebbian learning: links between nodes that are often active together are strengthened, whereas links between nodes that are not often coactive get weaker and are pruned. In some of these

models, the degree of pruning of connections during learning approximately matches that seen during the course of human brain development. During exposure to patterned input (roughly equivalent to sensory stimulation), nodes become more selective in their response properties, and under certain conditions, clusters of nodes with similar response properties emerge. Thus, in these computational models, selective pruning plays a role in the emergence of clusters of nodes (localization) that share common specific response properties (specialization).

In order to explore developmental disorders, Oliver and colleagues made simulations with a simple cortical matrix model in which one or other of the parameters known to be important for the emergence of structured representations was deliberately changed. In this case, when the authors manipulated an aspect of the intrinsic structure of the network, the relative length of excitatory and inhibitory links, this initial state change totally disrupted the formation of structured representations. In other simulations, structured representations emerged, but were distorted in different ways relative to the typical development case. Oliver et al. (2000) aimed to generate taxonomy of the ways that structured cortical representations could go awry in development, with the long-term aim that some of these artificial developmental disorders could potentially map onto those that occur in the real world.

A criticism of the Oliver et al. (2000) approach, and several related models, is that while they could potentially provide an explanation at the level of brain structure and function, they do not capture the genetic, cognitive, and behavioral levels. Very recent models have begun the ambitious task of simulating from the genetic to the behavioral levels, albeit within a restricted domain of cognition (past tense acquisition) (Thomas et al., submitted).

## 11.9 IS: FUTURE CHALLENGES

To recap on the basis of the IS view, it argues that early in postnatal development, many areas begin with poorly defined functions, and consequently can be partially activated by a wide variety of sensory inputs and tasks. During development, activity-dependent interactions between regions result in modifications of the intraregional connectivity such that the activity of a given area becomes restricted to a narrower range of circumstances. As a result of becoming more finely tuned, small-scale functional areas become increasingly distinct from their surrounding cortical tissue, and this will be evident in functional imaging studies as increasing localization of function. In summary, according to the IS view, small-scale areas of cortex become tuned for certain functions as a result of a combination of factors, including (i) the suitability or otherwise of the biases within the large-scale region (e.g., transmitter types and levels, synaptic density, etc.); (ii) the information within the sensory inputs (sometimes partly determined by other brain systems); and (iii) competitive interactions with neighboring regions (so that functions are not duplicated).

To date, the majority of the research on the emergence of specialized functions in human cortex has focused on specific regions. However, it is clear from the IS viewpoint that the next step is to understand how networks involving different regions, each with their own different specializations, emerge. In other words, while understanding the functional brain development at the level of individual cortical regions is beginning, still the knowledge about how the larger scale of cortical function in terms of networks of regions develops (Johnson and Munakata, 2005) is lacking. This section reviews, some initial evidence and theory that may begin to address this intriguing issue.

However, before considering the empirical evidence, one needs to consider what makes a network of functional nodes more or less successful. A branch of mathematics called graph theory concerns itself with the relative efficiency of different kinds of networks. While it may seem at first that a lattice or grid pattern is the optimal design for a network, formal analysis of measures of local network connectivity and the average path length from one node to another show that so-called small-world networks are the most efficient (Bassett and Bullmore, 2006). In contrast to the grid pattern of streets found in many American cities, small-world networks are more like the clusters of small streets in a village that is then linked to other such villages by fast highways. Although the overall balance of the small local streets and highways can vary, most biological systems (and even the World Wide Web) are small-world networks. Several studies have shown the regional interconnectivity of the adult brain is a highly efficient small-world network, but how does this efficient network emerge?

The first piece of the jigsaw comes from recent work by Fair et al. (2007, 2009) who used functional connectivity analyses in fMRI to study resting state control networks in school-age children and adults. Their analysis allows them to infer the nature and strength of functional connections between 39 different cortical regions. They found that development entailed both segregation (i.e., decreased short-range connectivity) and integration (i.e., increased long-range connectivity) of brain regions that contribute to a network. In a similar study, the general developmental transition from more local connectivity to greater and stronger long-range network connectivity was confirmed using slightly different methods and 90 different cortical and subcortical regions (Supekar et al., 2009; but see Power et al., 2012; Van Dijk et al., 2012 for technical limitations of these analyses).

The decrease in short-range interregional functional connectivity is readily explicable in terms of the IS view. As neighboring regions of cortical tissue become increasingly specialized for different functions (e.g., objects vs faces), they will less commonly be coactivated. This process may also involve synaptic pruning and, as heard in the last section, has been simulated in neural network models of cortex in which nodes with similar response properties cluster together spatially distinct from nodes with other response properties (Oliver et al., 1996). Thus, decreasing functional connectivity between neighboring areas of cortex is readily predicted by models implementing the IS view. More challenging from the current perspective is to account for the increase in long-range functional connections.

A maturational explanation of the increase in long-range functional connectivity would suggest that this increase is due to the establishment or strengthening of the relevant fiber bundles. However, the increase in functional connectivity during development may occur after the relevant long-range fiber bundles are in place (see Fair et al., 2009; Supekar et al., 2009 for discussion). While increased myelination is likely to be a contributory factor, (1) myelination itself can be a product of the activity/usage of a connection (Markham and Greenough, 2004); and (2) a general increase in myelin does not in itself account for the specificity of interregional activity into functional networks that support particular computations (but see Nagy et al., 2004). Thus, the strengthening and maintenance of long-range brain connections is also likely to be an activity-dependent aspect of brain development. This raises the question of why and how do particular anatomically distant brain regions begin to cooperate in a functional network?

A key to answering this question may lie in scaling up the basic mechanisms of Hebbian learning. Instead of cells that fire together wiring together, regions that tend to be coactivated in a given task context strengthen or maintain the neural pathways between them. While each region is becoming individually specialized for a particular function, this intraregion change in tuning is modulated and influenced by its presence within an emerging network of coactivated structures. For example, in a task that requires visually guided action, a variety of visual and motor areas will be coactivated along with multimodal integration areas. If the task is repeated sufficiently often then these patterns of coactivation will be strengthened, and specialization of individual regions will proceed within this context of overall patterns of activation.

The second source of coactivation in the developing human brain is commonly overlooked – spontaneous activity during the resting state (with no current task demands). Although there has been great interest in the resting state or default network in adults, only recently has this been studied using fMRI in children (although there is a long history of studying resting EEG in children). It seems likely that the oscillatory resting activity of the brain, which probably occupies more waking hours than those when the child is engaged in any specific tasks, may play a key role in strengthening and pruning the basic architecture of long-range connections.

The third reason why anatomically distant regions may strengthen and maintain their connectivity relates to the fact that most of the long-range functional connections studied by Fair et al. (2007) involved links to parts of the prefrontal cortex (PFC). This part of the cortex is generally considered to have a special role during development in childhood and skill acquisition in adults (Gilbert and Sigman, 2007; Thatcher, 1992). Indeed, Prefrontal Cortex (PFC) may play a role in orchestrating the collective functional organization of other cortical regions during development. While there are several neural network models of PFC functioning in adults (e.g., O'Reilly, 2006), few if any of these have addressed development. However, another class of model intended to simulate aspects of development may be relevant both to PFC and to the issue of how networks of specialized regions come to coordinate their activity to support cognition. Knowledge-based cascade correlation (Shultz et al., 2007) involves an algorithm and architecture that recruits previously learned functional networks when required during learning. Computationally, this dynamic neural network architecture has a number of advantages over other learning systems. Put simply, it can learn many tasks faster, or learn tasks that other networks cannot, because it can recruit the knowledge (computational abilities) of other self-contained networks as and when required. In a sense, it selects from a library of available computational systems to orchestrate the best combination for the learning problem at hand. While this class of model is not intended to be a detailed model of brain circuits (Shultz and Rivest, 2001; Shultz et al., 2007), it has been used to characterize frontal systems (Thivierge et al., 2005) and may capture important elements of the emerging interactions between PFC and other cortical regions at an abstract level. In addition, it offers initially attractive accounts of (1) why PFC is required for the acquisition of new skills; (2) why PFC is active from early in development, but also shows prolonged developmental change; and (3) why early damage to PFC can have widespread effects over many domains.

Although much work remains to be done to understand in more detail, the factors that lead to the emergence of long-range networks, the graph theory analyses of changes during the school-age years are generating important insights. While, as described earlier, there are differences in the balance of short and long connections between children and adults, it is important to note that the network organization of children's brains is

as efficient as that of adults. In other words, while children's brains are wired differently from those of adults, they are still optimally geared for the rapid and high-fidelity transmission of information. Whether the same is true in infancy and early childhood remains unknown.

Aside from the shift from local to long-range connectivity, another change in network structure observed using graph theory analysis during development is in the hierarchical structure. Adult networks have a more hierarchical structure that is optimally connected to support top-down relations between one part of the network and another (Supekar et al., 2009). While hierarchical networks have a number of computational advantages to be discussed below, they are known to be less plastic and more vulnerable to damage or noise in the particular nodes at the top of the hierarchy. Thus, the network arrangement of children may be more flexible and plastic in response to unusual or atypical sensory input or environmental context. Further, the response to focal brain damage, particularly in the prefrontal cortex, may be more clearly understood in the light of these different network structures.

One of the features of a hierarchical network is the capacity for one region to feedback highly processed sensory or motor input to the earlier stages of processing. In much the same way as we hypothesized that lateral interregional interactions help shape the intrinsic connectivity of areas to result in functional specialization, interactions between regions connected by feedback and feed-forward connections may also help shape the specialization of the areas involved. Top-down effects play an important role in sensory information processing in the adult brain (e.g., Siegel et al., 2000). For example, during perception, information propagates through the visual processing hierarchy from primary sensory areas to higher cortical regions while feedback connections convey information in the reverse direction. In a neurocomputational model of feedback in visual processing in the adult brain, Spratling and Johnson (2004) demonstrated that a number of different phenomena associated with visual attention, figure/ground segmentation, and contextual cueing could all be accounted for by a common mechanism underlying cortical feedback. Extending these ideas to development, there are potentially two important implications of feedback that will benefit from future exploration. The first of these will be to examine how the specialization of early sensory areas is shaped by top-down feedback, and vice versa, during development. The second topic for investigation will be to examine the consequences of relatively poor or diffuse cortical feedback in the immature cortex.

Top-down feedback from PFC may also have a direct role in shaping the functional response properties of posterior cortical areas. In cellular recording studies from both humans and animals, evidence has accrued that the selectivity of response of neurons in areas such as the fusiform cortex may increase in real time following the presentation of a stimulus. For example, McCarthy et al. (1997) measured local field potentials in face-selective regions of lateral fusiform cortex in human adults and found that responses of these neurons go from being face selective at around 200 ms after stimulus presentation, to being face identity or emotion selective at later temporal windows. This suggests that top-down cortical feedback pathways, in addition to their importance in attention and object processing (Spratling and Johnson, 2004, 2006), may increase the degree of specialization and localization in real time, as well as in developmental time. Thus, some of the changes in functional specialization and localization seen in face-sensitive regions may reflect the increasing influence of interregional coordination with other regions, including the PFC.

A final aspect of the transition from child brain network to the adult one is the greater connectivity between cortical and subcortical structures seen at younger ages (Supekar et al., 2009). This observation may be fundamental for our understanding of the emergence of the social brain and memory systems as it implies that the specialization of some cortical areas may be initially more dominated by structures such as the amygdala and hippocampus. As adulthood is approached, more networks become intrinsic to the cortex and develop a complex hierarchical structure more dominated by PFC.

## 11.10 SUMMARY, CONCLUSIONS, AND RECOMMENDATIONS

Now that DCN has become established as an interdisciplinary field in its own right, it has become time to evaluate and question the directions one is going in. One of the most common criticisms leveled at the newly emerging field is that it is primarily being driven forward by the powerful new methods for imaging brain structure and function in an infant- and child-friendly way (as well as new techniques for genetic analyses), and that it lacks the theory-driven approach that characterizes much of the best work in cognitive development. Similar concerns are expressed, albeit less directly, by students who can be daunted by the somewhat fragmentary islands of data that have been acquired to date about human functional brain development. Where is the overarching theory or framework within which they can make sense of disparate observations? A related concern sometimes expressed by those in cognitive science is that the hypotheses which are presented in DCN are reductionist, or otherwise impoverished as a cognitive explanation of infant or child behavior. In other words, this criticism is that what hypotheses and theories there are in the field are of the wrong type, and do not offer a

satisfactory explanation of behavioral change in development.

Starting with the criticism of a relative lack of theories in DCN, acknowledgement has to be made that, at least compared to the parent discipline of cognitive development, work in DCN is generally less theory driven (albeit with the exceptions discussed in this chapter). Why is this? A large part of the explanation is believed to be due to the sudden increase in the volume and diversity of data available because of the new methods that have become available. Many theories that successfully accounted for sets of behavior observations in child development founder on the rocks when attempts are made to account for neuroscience data relating to the same behavioral tasks. For one thing, when one more than doubles the quantity of data to be accounted for, then many previously successful theories will no longer offer a satisfactory explanation, simply because the chance of observing refuting evidence is much higher. Bringing powerful new methods into a field is analogous to a catastrophic environmental change during evolution – the majority of species (theories) simply cannot adapt and, therefore, die off. It takes generations for the better-adapted species to emerge.

The second issue is that of accommodating to new types of data. When one begins to study brain function directly, the first thing that strikes is the complexity of the processes involved. For example, neuroscience evidence indicates that the brain has at least three partially independent routes for executing eye movements. While these routes may have slightly different attributes, duplication of computations and (apparent) redundancy seems to be a basic feature of how the brain does things. Thus, at a sweep, simple single-route cognitive models appear less plausible. Add to this the complexity of feedback routes interacting with sensory-driven information, and the undoubted importance of temporal synchrony, and many existing theories of cognitive development look hopelessly simplistic. Of course, a common reaction to this is that theories of cognitive development are not intended to account for neuroscience data – that is, merely a matter of implementation. However, if you accept this argument, I contend that you are not doing DCN (and I would argue that satisfactory explanations of development necessitate bridging between levels of observation (see Johnson, 2010)).

This leads us to the second common criticism of theory in developmental science; the theories are of the wrong type to be of relevance for explaining the development of human behavior. Commonly, the view is expressed that theories in DCN are reductionist and, therefore, do not offer good explanations of cognitive change. As discussed earlier, it has been argued following Marr (1982), that cognition is a level of explanation independent from the underlying neuroscience. Recent directions in neuroscience suggest that, to the contrary, there is a large degree of interdependence between levels in real complex biological systems such as the brain. This has led to the proposal that theories that are consistent between different levels of explanation should be sought (see Mareschal et al., 2007, for a detailed discussion of this point). Ultimately, theories that are consistent with both behavioral and brain development evidence will have greater explanatory power than those confined to one level of observation.

In considering the issues above, the current dearth of plausible theories in DCN seems unsurprising. After all, new fields in the biological sciences (in contrast to some physical sciences) often go through a natural history phase in which collection of basic data is the priority. However, in this chapter, it was argued that one needs to strive to bring more adequate and appropriate theories into the field. Thus, three positive suggestions for hallmarks of a good theory in DCN are offered.

1. The theory advanced should genuinely relate neural observations to behavioral ones, and can be equally well tested (and refuted) by either neural or behavioral level observations. I suspect that a variety of different types of theories will emerge to serve this bridging function, but that they are unlikely to look like many existing cognitive development theories. Theories that have been developed purely on the basis of behavioral data are unlikely to naturally map on to brain imaging data, and there is a danger in seeking only confirmatory data. Ideally, theories of functional brain development that are equally compatible with brain and behavioral observations should be developed.
2. Theories in developmental science should involve mechanisms of change. This suggestion is not new (e.g., Karmiloff-Smith, 1998; Mareschal and Thomas, 2007), but it is still surprisingly common to see theories that explain the state of affairs before and after a developmental transition, but that do not specify the mechanisms of the transition itself (other than using the terms such as maturation or learning). Theories of development need to be theories focused on change.
3. Given that theories in DCN are accounting for several levels of observation, and that they also need to be compatible with undoubtedly complex and dynamic aspects of neural processing, we need to find ways to elucidate and present those theories so that they are both comprehensible and clarifying. This is the attraction and importance of formal computational modeling, be it symbolic, connectionist or hybrid (see Mareschal et al., 2007). While theories may initially develop as informal ideas, ultimately we should aim to implement them as computational models.

Finally, the author cautions against being too prescriptive. In the long term it is probably good for the field to have a heterogeneous mix of different types of theories and let the data, and time, select those with the best fit to reality. After all, despite their prolonged domination, the dinosaurs did not inherit the globe.

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