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Author(s): Mark H. Johnson

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## Functional Brain Development in Infants: Elements of an Interactive Specialization Framework

*Mark H. Johnson*

One future direction for cognitive development research involves a closer integration with our knowledge about the developing brain. I present a framework for analyzing and interpreting postnatal functional brain development in human infants. Three specific hypotheses contribute to this framework, within which a variety of phenomena associated with the neural basis of perception and cognition in normal and abnormal development can be characterized.

### INTRODUCTION

Over the past decade there has been increasing interest in relating behavioral changes during infancy to underlying changes in the brain, and in particular to the postnatal development of the cerebral neocortex (e.g., Diamond, 1991; Johnson, 1997a, 1997b; Nelson & Bloom, 1997; Richards, in press). Aside from the potential clinical benefits, increased knowledge of the relation between the developing brain and behavior may change ideas and theories about the mechanisms underlying perceptual, motor, and cognitive development. In addition, the increasing availability of methods for imaging the brain at work will allow us to study the neural basis of cognitive ability during childhood much more readily. It will therefore be necessary to develop theories about the functional development of the brain that allow us to integrate information about the structural (neuroanatomical) development of the brain with data about perceptual, cognitive, and behavioral changes.

Many of the efforts so far to relate brain to behavioral development have been based on a maturational framework in which it is assumed that as particular regions of the brain mature they allow or enable new sensory, motor, and cognitive functions to appear. A related assumption has been that there is a progression of maturation from posterior to anterior regions, with the primary visual cortex being functional from shortly after birth and the frontal lobes, and prefrontal cortex, being the last parts to become functional. This posterior-to-anterior assumption is largely based on evidence from structural neuroanatomical studies (see Johnson, 1997a, for review), but it is assumed to have direct functional consequences.<sup>1</sup> I suggest that in the forthcoming decades we have to move beyond

the maturational framework. In this paper I present elements of an alternative framework (way of thinking) for postnatal functional cortical development. This framework includes three specific hypotheses about postnatal functional brain development. Finally, I discuss the implications of this proposed view for developmental disorders and early brain damage.

A maturational framework underlies many current models that attempt to relate the physical growth of the brain to changes in behavior. For example, Johnson (1990) advanced a model of how the differential maturation of cortical pathways could explain changes in visual orienting and attention in human infants over the first six months of life. This model assumed that frontal regions (such as frontal eye fields) were on the last pathway to mature and in general corresponded to a posterior-to-anterior maturational progression. While neural and behavioral evidence available at the time corresponded well with predictions of the model, more recent studies suggest that frontal structures may be playing an active role earlier than more posterior structures. For example, in studies of saccade-related potentials in 6-month-olds we have observed eye-movement related potentials over frontal sites but not over the more posterior sites where they are observed in adults (Csibra, Tucker, & Johnson, 1998, in press). Converging results are obtained when eye-movement tasks are studied in infants with perinatal focal damage to cortex: it is infants with damage to the frontal quadrants of the brain who show deficits, and not those with more posterior damage which produces such deficits in adults (Johnson, Tucker, Stiles, & Trauner, 1998).

To briefly preview the framework to be presented, I argue that functional brain development can be analyzed in terms of the differential specialization of multiple coactive pathways. In addition to differential

<sup>1</sup> By "functional" in this paper, I refer to the information-processing properties of the neural circuits in question, and not to basic physiological functions associated with maintaining cells.

specialization *between* brain pathways, I hypothesize that differential patterns of specialization *within* a pathway can occur during development, sometimes resulting in patterns and temporal dynamics of the neural basis of behavior in infants that differ from those observed in adults. These differences in the neural control of behavior in infants can be empirically observed and may help make sense of some currently puzzling data.

While the hypotheses presented can be tested independently, together they form the basis of a framework for a new way of thinking about functional brain development in infancy within which more specific models dedicated to particular domains can be developed. What is presented here is far from a complete theory of functional brain development in infants, but it is intended to set a direction and agenda for future research.

## ISSUES AND ASSUMPTIONS

*Background issues.* Gottlieb (1992) distinguished between two approaches to the study of development. The first of these, "predetermined epigenesis" assumes that there is a unidirectional causal path from genes to structural brain changes to psychological function. In contrast, the second approach, "probabilistic epigenesis," views interactions between genes, structural brain changes, and psychological function as bidirectional. Integral to the latter approach is the importance of activity-dependent development. One manifestation of this in postnatal life is that infants themselves select appropriate inputs for the subsequent further specialization of their brains (Johnson and Morton, 1991). As discussed above, much current theorizing on the neural basis of sensory, motor, and cognitive change, is based on the view that the maturation of particular neocortical regions or pathways allows or enables new functions to appear (e.g., Diamond, 1991; Johnson, 1990). This clearly follows a predetermined epigenesis viewpoint in which the primary cause of a cognitive change is neural maturation.

A number of recent reviews of pre- and postnatal brain development have concluded that probabilistic epigenesis is a more appropriate way to view postnatal brain development (and also prenatal development, though that is not the topic of this paper) (e.g., Johnson, 1997a; Nelson & Bloom, 1997). Explaining developmental change when there are bidirectional interactions between brain structure and (psychological) function is, however, more challenging. Possibly the recent advent of connectionist modeling will offer a formal way to analyze interactions between neural structure and function (Elman et al., 1996). When

adopting a probabilistic epigenesis viewpoint, the aim is still to unite developmental neuroanatomical observations with functional development. Until we have more detailed knowledge of the bidirectional relations between structure and function, however, it would be unwise to use structural neuroanatomical data to constrain theories of functional brain development too closely. In a related manner, a probabilistic epigenesis approach emphasizes the need for notions of *partial functioning* of neural pathways because in order for bidirectional interactions between brain structure and function to work, there needs to be early partial functioning which then shapes subsequent structural developments. From this viewpoint, then, structural and functional changes in regions of the cortex codevelop. It does not appear to be the case that cortical regions are functionally silent before they become mature in terms of their neuroanatomical structure.

In contrast to some other regions of the brain, it is clear that the cerebral cortex shows structural and functional changes well into postnatal life in humans (see Johnson, 1997a, for review). It is also the part of the brain most commonly associated with higher cognitive functions, and therefore likely to have central importance for cognitive and perceptual development. The general neuroanatomy of the neocortex is remarkably similar across both regions and species. It remains controversial to what extent the detailed differences in neuroanatomy sometimes detectable between and within regions of the neocortex are the result of prenatal genetic and molecular factors, or the result of pre- and postnatal neuronal activity-dependent processes (see Johnson, 1997a, for review).

Although it is not feasible to use functional brain imaging methods such as positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) with young infants, it is possible to use scalp recorded event-related electrical potentials (ERP). Recent advances in this technology allow recording with high-density arrays for improved spatial resolution (Tucker, 1993). This method is thought to detect electrical changes, as groups of neurons fire within the cerebral cortex. It thus provides a good method for studying the time course and spatial distribution of functional activity in cortex.

*Assumptions.* A number of specific assumptions underlie the framework to be presented, all of which have at least some supporting evidence. The first of these is that from shortly after birth multiple pathways and structures within the cerebral cortex can be partially activated by stimulus presentation or task situations. Whether this includes the entire set of pathways and structures available to the adult for in-

formation processing is unknown. It is assumed that in the newborn, while major cortical pathways, such as the dorsal and ventral routes of visual processing, are relatively immature, neurons on the pathway are capable of being activated and of transmitting information to output centers of the brain. While even in the adult multiple pathways are potentially engaged in a range of tasks, particular pathways appear to dominate, in the sense of most directly controlling behavioral output in specific task contexts. An example of this comes from the study of the neural basis of eye-movement control. Schiller (1998) describes multiple pathways that are involved in eye-movement planning and control in adult primates. In specific task situations, however, such as making an anticipatory eye movement to an expected target location, a particular subset of these pathways dominate the response of the subject.

The next assumptions relate to why particular pathways dominate the behavioral response in particular stimulus or task situations. It is assumed that two temporal factors are important here: the relative speed of processing for a given type of information in different pathways, and the speed of response of the subject. Behavioral responses are partly guided by the information processed when the action is initiated. A delayed response allows slower pathways to influence the response. Rapid reactions are made on the basis of faster, more automatic, brain pathways. For example, in tasks in which adult participants are required to make eye movements to a series of visual targets, pressure to respond rapidly can lead to systematic errors generated by more reflexive eye-movement pathways (Dassonville, Schlag, & Schlag-Rey, 1992), some of which are subcortical (Schiller, 1998).

## AN INTERACTIVE SPECIALIZATION FRAMEWORK

*Hypotheses.* In this section, I present three inter-related working hypotheses that contribute to the position I wish to advance. I first summarize these hypotheses and then examine each in more detail.

1. Cortical pathways differ from each other by virtue of their particular pattern of inputs and outputs to other brain structures and biases in their information-processing properties. The latter refer to slight differences, such as those in the detailed patterns of intrinsic connectivity, the balance of neurotransmitters, or synaptic density. Such differences correspond to those that Elman et al. (1996) referred to as "architectural constraints." In the newborn, however, they are

thought to be slight biases on a very similar, general, immature neocortical architecture. These initial biases are sufficient to ensure that particular types of sensory input, or input-output pairings, are more efficiently processed by a subset of the pathways. There is thus a process of "recruitment" of particular pathways and structures for certain functions.

2. During development, cortical pathways and structures go through a process of specialization. By specialization I mean the extent to which a given cortical region is selective in its response properties. Shortly after birth a cortical region may respond to a wide variety of visual stimuli, but with development the same region may only be engaged by a subset of these stimuli. This process may be somewhat akin to the tuning of response properties of single neurons. I hypothesize that in addition to narrowing response properties, the process also facilitates speed of processing for the stimuli or task situations on which it becomes specialized.
3. Specialization within a cortical pathway does not necessarily proceed from sensory input to output during development. In at least some cases the process starts at later stages of the cortical processing stream and progresses to earlier (shorter latency) stages.

The first hypothesis outlined above is that initial biases in the different pathways activated, along with the patterns of connectivity of these pathways to other parts of the brain, lead to some pathways and structures being marginally more suited to processing information about some kinds of input, or input-output relations. Hypothesis 1 suggests that in the newborn infant few, if any, of these cortical pathways are specialized (in the above sense) for most tasks, but by virtue of initial biases some are engaged more than others by particular tasks or stimuli. Hypothesis 2 asserts that these initial biases are then greatly amplified by a subsequent process of specialization. This notion further specifies the view initially advanced by Elman et al. (1996) that cortical structures are "recruited" for computational functions during development.

Specialization refers to the extent to which a given cortical region is selective in its response properties (Johnson, 1999), and is related to the notion of "perceptual narrowing" previously described by Nelson (1993). For example, a recent high-density ERP study investigated the effects of inversion on face processing in infants and adults. The "inversion effect" refers to the observation that inverted faces activate neural

and cognitive mechanisms different from those activated by upright faces. De Haan, Oliver, and Johnson (1998) found that infants at 6 months showed the same "inversion effect" with monkey faces as they do with human faces, a finding consistent with their processing human and monkey faces in the same way. In contrast, in adults, human face stimuli produce different patterns of activation from those produced by other species (de Haan et al., 1998). These results suggest that cortical processing of faces becomes more finely tuned (specialized) for human faces during human development.

While in this paper specialization is used to describe a particular type of change in development, there are several plausible neurocomputational mechanisms which could underlie it. One likelihood is that it involves the selective pruning of inappropriate synaptic connections, and possibly also inhibition of other alternative pathways (Jacobs, 1999; Shrager & Johnson, 1996). For the purposes of the present framework, the mechanisms underlying specialization need only be sufficient to cause particular cortical pathways to become more adept than other pathways (which were initially alternative and coactivated pathways) at processing a particular class of stimuli.

*Predictions and supporting evidence.* In this section I explore some predictions and implications of the framework presented, and use it to account for a number of phenomena associated with postnatal functional brain development in human infants. The three sets of phenomena I will focus on are:

1. Changes in *localization* during development, that is, developmental changes in the extent of cortex activated following presentation of a stimulus or a task situation.
2. Evidence that infants often act before fully processing information relevant to the action.
3. The precocial involvement of some frontal cortical regions during early infancy.

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 both for word learning (Neville, 1991) and face processing (de Haan et al., 1998) there is increasing localization of processing of a stimulus class with age/experience. That is, a larger area of the scalp shows a stimulus-specific effect in younger infants than in older ones. Within the present framework, such changes may be attributed to more pathways being partially activated before experience with a class of stimulus leads to the specialization of one or more of those pathways. In the example of face processing, both the left

and the right ventral visual pathways are differentially activated by faces in early infancy, but in many (but not all) adults this localizes further to the right ventral pathway only (Johnson & de Haan, in press). In the example of word recognition, differences are initially found over widespread cortical areas, but become localized to left temporal leads after further experience with this class of stimulus (Neville, 1991). Thus, changes in localization can be viewed as a direct consequence of specialization. Fewer pathways become activated by a given stimulus because most of them become tuned to other functions and therefore are no longer engaged by the broad range of stimuli they responded to earlier in development. Additionally, it is possible that there is inhibition from pathways that are becoming increasingly specialized for that function. In this sense, then, there is competition between pathways to recruit functions.

The second class of phenomena that can be interpreted within the framework outlined above concerns the relative temporal dynamics of alternative cortical routes of information processing. Given that more cortical pathways may be activated in infants, how is it that their behavior shows evidence of deficits in processing relative to that of adults? I have already suggested that one part of the answer to this question lies in the lack of specialization of these pathways for computational functions suited to the information they process. I now suggest that another (and related) part of the answer lies in the speed with which these pathways act to influence output.

Many ERP studies with infants have shown that differences between trial types (such as words and nonwords) are found at much longer latencies in infants than in adults. For example, face-sensitive effects in the ERP occur around 170 ms after stimulus onset in adults, but are not observed until around 350 ms in 6-month-old infants (de Haan et al., 1998). It is widely assumed that such differences are due to slower neural conduction rates in the infant brain, but recent spatiotemporal analyses of high-density ERP recordings suggest that this may be only one part of the story. Specifically, infants may show longer latency effects because specialization occurs later in their cortical processing stream than it does in adults.

One line of evidence consistent with this account comes from the fact that the early visually evoked potentials (VEPs) to foveal stimuli are only slightly delayed in 6-month-olds relative to adults, suggesting that at least for these early components of cortical visual processing neural processing speed is only one contributory factor. A second line of evidence comes from the spatiotemporal analyses of the ERP produced when an infant views faces which suggest that

the face-specific response occurs at a later stage of cortical processing in infants than in adults. Both infants and adults show three distinct temporal phases in their cortical response to complex visual stimuli. While adults show face-sensitive responses at the second of the three stages, it is not until the third phase that infant ERPs to faces differ from those to other stimuli. Thus, in at least this case, the face-specific response occurs much later in time in the infant than in the adult partly because it takes further stages of cortical processing to achieve a selective response.

If we extend this observation from face processing to other domains, it raises the further hypothesis that specialization (in the sense defined above) begins at later real-time stages of cortical processing (commonly those regions more associated with output), and, with experience, moves forward in real time to early stages of the processing (commonly associated with analyzing sensory input). Since parts of the frontal cortex have major outputs to subcortical regions to control behavior, and since the frontal cortex appears to be the terminal cortical structure for many pathways (Fuster, 1989), I speculate that this region may show evidence of specialization (stimulus selectivity) before many other cortical regions. This prediction stands in contrast to the currently prevailing view that frontal, and especially prefrontal, cortical regions are the last to show functional activity in human postnatal brain development.

It is important to clarify that these claims do not call into question specific hypotheses about the relation between prefrontal cortex development and performance in several detour and occluded object reaching tasks toward the end of the first year of life (e.g., Diamond, 1991). They merely suggest that other associations between frontal and prefrontal development and behavioral performance will be found at younger ages. Some preliminary indications of this come from recent high-density ERP studies of saccade-related potentials in 6-month-olds. As mentioned earlier, Csibra and colleagues (1998, in press) examined the cortical activity associated with the planning of eye movements in 6-month-olds and observed eye movement related potentials over frontal sites, but not over the more posterior sites where they are observed in adults (see also Richards, in press). Converging results are obtained when eye movement tasks are studied in infants with perinatal focal damage to cortex. Infants with damage to the frontal quadrants of the brain show deficits in such tasks, whereas those with more posterior damage, which causes such effects in adults, do not (Johnson et al., 1998; see also Craft, White, Park, & Figiel, 1994).

To summarize the related hypotheses presented so far, in the first few weeks after birth many brain path-

ways are partially activated by task situations in infants, but most or all of the cortical pathways are unspecialized. Action in young infants is therefore often based on the output from the first available pathway, which may often result in an impoverished or incorrect response when the task situation is more complex or demanding. In very young infants, subcortical pathways will often be faster than any of the cortical routes, and may thus dominate behavioral responses. With further age/experience, pathways become more specialized and therefore fewer of them are initially activated in a given stimulus/task context (resulting in increased localization). Those that remain activated, however, may compete more vigorously to control action. At this later stage, the child has more options available for guiding action appropriately. For example, by delaying action, the child can bring more complex representations to bear on behavior. By adulthood, more specialized pathways mean that fewer pathways are engaged by a task situation (although it is still likely to be more than one), and response time (imposed by task demands) may determine which pathway guides the action.

*Disorders and deviations.* We can use the framework outlined above to consider (1) the effects of early brain damage, and (2) developmental disorders of known or suspected genetic etiology. Starting with the former, it should be evident that the framework presented allows for the possibility that, prior to the specialization of the relevant pathways, other pathways that are also initially activated by the same stimulus/task can compensate for the damaged pathway or region. In other words, pathways have the capacity to specialize for a variety of functions. It is important to note that the same process of specialization that would occur normally is involved, albeit with a different allocation of functions to pathways. It is likely, however, that in at least some domains there will be some cost to the reallocation of pathway specialization given that functions will not always be allocated to pathways with the optimal initial biases and/or connectivity to other regions.

Although the effects of early focal lesions on cognition are often variable, complex, and domain dependent, at least in the area of effects on language acquisition some general conclusions can be reached (Stiles & Thal, 1993).

1. Regions of the left temporal lobe may be best suited to language processing, but they are not critical since language can develop in close to normal ways with this region damaged.
2. Focal pre- and perinatal lesions often cause delay regardless of the site of the lesion.

3. Different regions of the cortex may be involved in the acquisition of language in infants from those that are important for language in adults. Specifically, there may be changes in the extent and pattern of lateralization as well as changes along the anterior–posterior axis.

These general conclusions are largely consistent with the framework outlined above in that prior to the specialization of relevant pathways, other pathways can specialize in their place in the event of damage. For example, right ventral visual pathways (such as those that normally specialize for face processing) could be replaced by left ventral visual pathways in the event of early damage. Such rearrangements of the normal patterns of specialization are likely to have some general cost even on other domains, however, since there are fewer pathways available for specialization and the rearrangement of specialization may not be optimal.

The observation that the cortical regions critical for a function may change during acquisition is also broadly consistent with hypothesis 3, which states that specialization within a pathway sometimes progresses from cortical output regions toward those closer to input structures. If the patterns of specialization within a pathway are different for infants from those seen in adults, we would expect differences between infants and adults in the effects and locations of lesions that cause effects.

With regard to developmental disorders of genetic etiology, it would be premature to offer any explanations of specific disorders. With a framework such as that presented here, however, we can reverse the form of question normally asked about such disorders. Instead of seeking specific explanations for particular disorders, we can inquire what the characteristics of “theoretical” disorders would be following different types of deviation within the framework (see also Oliver, Johnson, Karmiloff-Smith, & Pennington, 2000). At a later stage it would then be valuable to assess the extent to which certain real disorders might share these characteristics. For example, one type of deficit could involve defects in the molecular mechanisms underlying the specialization process itself. In terms of the neural substrates of behavior such disorders would manifest as “arrested development” with many relatively unspecialized pathways still competing for influence over behavior, a situation which would presumably result in variable and poor performance over a range of tasks. Other kinds of disorders could possibly affect particular pathways, and compensation by other pathways could come into effect in a way similar to that following early focal damage. Behaviorally, patterns of mild deficit could result from

this. More cognitive-specific kinds of disorder could result from subtle molecular and cellular distortions that change some of the initial biases in some pathways. Thus, the normal patterns of biases that eventually result in the characteristic adult allocation of functions to pathways would be altered, resulting in a different neural basis for behavior even when near normal behavioral competence is achieved (see also Karmiloff-Smith, 1998). A more detailed account of how differing initial biases can alter the nature of the functions that subsequently emerge has been presented elsewhere (Oliver et al., 2000).

## CONCLUSIONS

In this paper I have presented a framework for the analysis of postnatal functional brain development. The framework has a number of implications for views on cognitive and behavioral development in infancy. As opposed to stage-like transitions between levels of cognitive ability, the framework encourages cognitive models with multiple competing representations that are engaged by particular stimuli or task demands, and which compete to influence behavioral output. Such models are already being generated. For example, Mareschal, Plunkett, and Harris (1999) have modeled behavioral data concerning infant responses to occluded objects in a connectionist network model with two pathways which are differentially activated by tracking either an object’s spatiotemporal properties or its surface features. During the next decades, I anticipate great advances as we come closer to incorporating evidence from neuroscience into our understanding of mental development in infants and children.

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## ADDRESS AND AFFILIATION

Corresponding author: Mark H. Johnson, Center for Brain and Cognitive Development, School of Psychology, Birkbeck College, University of London, London WC1E 7HX, United Kingdom; e-mail: mark.johnson@psyc.bbk.ac.uk.

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