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Developing Brain Networks of Attention

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Abstract

Purpose of Review—Attention is a primary cognitive function critical for perception, language, and memory. We provide an update on brain networks related to attention, their development, training and pathologies.

Recent Findings—An executive attention network, also called the cingulo-opercular network, allows voluntary control of behavior in accordance with goals. Individual differences among children in self regulation have been measured by a higher order factor called effortful control (EC) which is related to executive network and to the size of the anterior cingulate cortex.

Summary—Brain networks of attention arise in infancy and are related to individual differences including pathology during childhood. Methods of training attention may improve performance and ameliorate pathology.

Keywords

Attention networks; fMRI; DTI; methylation; myelination; pathology; plasticity; temperament

Introduction

In this review we discuss recent studies providing new information about brain networks related to attention. This includes studies of how the brain changes as attention networks develop in infancy and childhood. We then consider implications of the development of attention for some forms of pathology. Finally, we discuss whether and how brain networks related to attention can be changed by training.

Development of Attentional Networks

The Attention Network Test (ANT) is designed to measure brain networks related to alerting, orienting and executive control [1**]. Figure 1 summarizes the anatomy, timing and chemistry of each of these networks. Alerting has been related to the norepinephrine system which modulates frontal and parietal structures [1**]. Recent studies have shown the role of posture on alerting [2] and found evidence of top down executive control on the maintenance of alerting [3*].

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Orienting to sensory stimuli has been shown to involve the frontal eye fields and areas of the superior and inferior parietal lobe [1**]. A recent study shows the importance of connectivity between the left and right parietal lobes in orienting to visual stimuli [4*].

The brain's executive attention network involves the anterior cingulate and anterior insula (operculum) [1**] and is called cingulo-opercular network in fMRI studies [5**]. The executive network is involved in error detection, resolving conflict and other aspects of performance [5**, 6, 7]. The executive network is present in infancy, with the areas activated by perceived error similar in adults and infants, including the anterior cingulate cortex (ACC) [8]. However, evidence suggests that these areas do not connect with or control motor output until about age 4 [6]. Before this time control is exercised chiefly through orienting [6]. An fMRI study [9] of 750 persons from 4 to 21 years found that in early childhood the size of the right anterior cingulate is the best predictor of the ability to resolve conflict, as measured by reaction time differences between congruent and incongruent flankers. Later in development diffusion tensor imaging suggests that overall reaction time is most related to the efficiency of white matter connections.

Performance on tasks using each of these three networks improves during childhood [1**]. Imaging indicates that their anatomies, while distinct, can interact to influence performance [10*,11]. During development, the scores for these networks have also been related to individual differences in temperament as measured by parent reports of their child's degree of effortful control, negative affect, and surgency [6, 12,13**].

The ability to image connectivity by using correlations between activations of remote areas during the resting state (functional connectivity) and by use of diffusion tensor imaging (DTI) has created a subarea of connectomics within developmental and cognitive neuroscience [14**]. A review paper [14**] summarizes the major features of early brain development from animal and fMRI studies: (a) neurogenesis and axonal growth prior to birth, (b) synaptic connections established rapidly after birth, and (c) a period of consolidation including cell loss and synaptic pruning, as well as increasing white matter due to improved connectivity through myelination.

Graph theory has been used to trace the development of specific networks from infancy [15*] to adulthood [16]. Most of the graphical depictions of changed connections use functional imaging, examining correlations among various sites, mainly from resting MRI but some studies use DTI. According to [14**] there is convergence of these methods on points such as the existence of many networks at birth, the abundance of short connections in early development, and later the relatively fixed state of these networks (but see also our section on training). While an increase of long connections over development is often reported in functional imaging studies, most DTI studies show mainly increased axonal density and myelination in later development [14**]. Improved axonal efficiency, however, might differentially favor longer connections.

It is not always easy to relate findings of changes in brain connectivity to the obvious changes in behavior and self-regulation occurring between infancy and later ages. Many studies using questionnaires or behavioral tests that measure effortful control (EC) show

evidence of increasing self regulation at least until late childhood [1**,6]. These findings fit fairly well with the functional connectivity results of more efficient long connections [15*, 16]. There is controversy about many of these findings [14, 17], and one reason for varied results may be that gene expression interacts with experience during development. For example, randomly assigning people with different genetic polymorphisms to interventions has provided evidence that genes interact with the quality of parenting to influence changes in behavior during early life [18*]. The findings that gene expression interacts with experience during development suggests the possibility that interventions might improve the functioning of brain networks.

Pathology of Attentional Networks

Parent reports of their infant's temperament at 7 months were correlated with the child's performance on the ANT at 7 years [6], for example, performance on the executive network at age 7 years was related to parent reports of positive affect at 7 months [6]. Temperament ratings have also proven useful in describing pathologies of attention [12,13**]. Using dimensions of temperament, one recent paper describes three subtypes of attention deficit disorder: surgent, irritable and mild [13**]. Children in the irritable subtype had high negative affect. Those in the mild subtype had low effortful control. While children in the surgent type had higher impulsivity than controls, they had lower surgency than other ADHD types. These temperamental characteristics were related to brain areas through imaging. Based on their results the authors argued for a close relationship between the subtypes of ADHD and attention networks, but more and larger samples are still needed for confirmation.

A developmental approach to pathology that is poised to advance our understanding involves longitudinal observations in typical and pathological states to determine when the pathology has its effect on brain activity. For example, a longitudinal study of children diagnosed with child onset schizophrenia [19] found an abnormal trajectory of reduced cortical thickness emerging in cingulo-fronto-temporal connections between ages 10 and 20, when for many patients schizophrenic symptoms emerge. Whether these developmental differences are due to the disease or treatment is unclear. However, this does confirm the likely importance of the executive attention network in the progression of the disorder.

A study of the emergence of anxiety during adolescence emphasizes a developmental approach to genetic influence on pathology. A common polymorphism related to decreasing endocannabinoid signaling influences frontolimbic circuitry at about 12 years of age and is related to anxiety disorders emerging at that time [20**]. Using a knock in mouse model, similar effects were also found in adolescent mice supporting the human studies [20**]. This study shows the importance of relating the timing of symptoms to the underlying circuitry of the disorder.

Autism has long been associated with deficits in orienting of attention in both social and nonsocial situations [21]. A recent meta-analysis of DTI studies of autism spectrum disorder [22] in comparison with normal subjects supports a theory of reduced long fiber connectivity in patients, particularly in the corpus callosum and the longitudinal and uncinate fasciculi.

Although the meta analysis supported hypoconnectivity in autism [22], other studies suggest the opposite [23]. One study finds that autistic individuals show hyperconnectivity of the orienting network during childhood but hypoconnectivity as adults, indicating again the importance of a developmental approach [24*] to resolve this issue. Connectivity problems have also been associated with other disorders known to the orienting network such as Alzheimers Disease [25] and brain injury [26].

Training of Attentional Networks

Among the many behavioral changes that occur with development is the greatly increased speed of responding during various tasks. This fact has been well documented in the literature, for example, at age 7 the ANT has an overall reaction time 400 millisecon longer than for young adults [27, 28]. Attention training studies have sought to improve the function of attention networks in infants [29] and young children [30,31*,32] by exercises that practice use of the network or in adults by changing brain states through exercise [33,34**] or meditation [35]. The studies have observed that following training, electrical recording showed that the executive network was more similar to adults than it was for non-trained children and there was some generalization to other cognitive functions such as self control and IQ [30,31*]. The generalization of training to remote tasks and daily life remain controversial, however.

Training of adults in mindfulness meditation has used DTI to show specific improvements in white matter pathways surrounding the anterior cingulate following 2 to 4 weeks of training [35]. We speculate that these changes may be induced by the frontal theta rhythm which is increased following meditation training [28] or by appropriate stimulation [36, 37].

In an important paper, evidence for white matter changes during learning was summarized and related to changes in the speed of responses [38**]. Studies using DTI have shown changes in fractional anisotropy (FA) thought to reflect the efficiency of white matter during various forms of learning. Studies showing FA change include training of working memory, meditation, juggling and other human tasks [39**]. Most of these studies have concluded that the white matter change was due to myelination.

There is also evidence from a study of mice learning to run on a wheel with irregular spokes, requiring acquisition of a new and complex motor skill. This form of learning was shown to activate precursor oligodendrocytes in mice [40]. When activation of the oligodendrocytes was blocked, the animals did not learn, showing the importance of cells producing myelin for acquiring a motor skill [40].

There are important individual differences in the amount of improvement one finds in training [28]. One source of these differences may be genetic polymorphisms in the efficiency of methylation that could lead to myelination differences [27,41]. It has been shown that adults with the T allele of the MTFHR gene have less efficient methylation and show poorer performance in speeded attention tasks [27]. Future studies will be needed to determine whether these changes are due to epigenetic mechanisms or to other effects of methylation efficiency on performance.

Many forms of substance abuse may involve deficits in self control. There is evidence that a month of meditation training may reduce addiction to tobacco, even when there is no conscious intention to quit smoking [42]. If this finding replicates in larger samples and for other forms of addiction, it may be an important connection between the accumulating evidence of training attention networks and an important public health problem.

Conclusions

Brain networks of alerting, orienting and executive control develop during childhood partly by improving the efficiency of long range connections. This finding provides an opportunity for pediatricians to follow the development of a critical set of functions in their young patients. The link between performance on reaction time tests that have been used in children as young as 4 years and questionnaires provide the opportunity to use non-invasive techniques to assess important landmarks in functional brain development.

Several important pathologies involve abnormalities of these brain networks and their connections, including autism, attention deficit disorder and schizophrenia. Moreover, connections can be influenced, at least to some degree, by training that involves repetition of the network or changes of brain state. Training may be useful in improving function and combatting some forms of pathology.

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Key Points

- Specific brain networks have been related to aspects of attention
- Each network develops in infancy and childhood
- Connectivity between neural areas play an important part in each network
- Some developmental pathologies are related to attention networks
- There is evidence that training can influence the efficiency of attention network

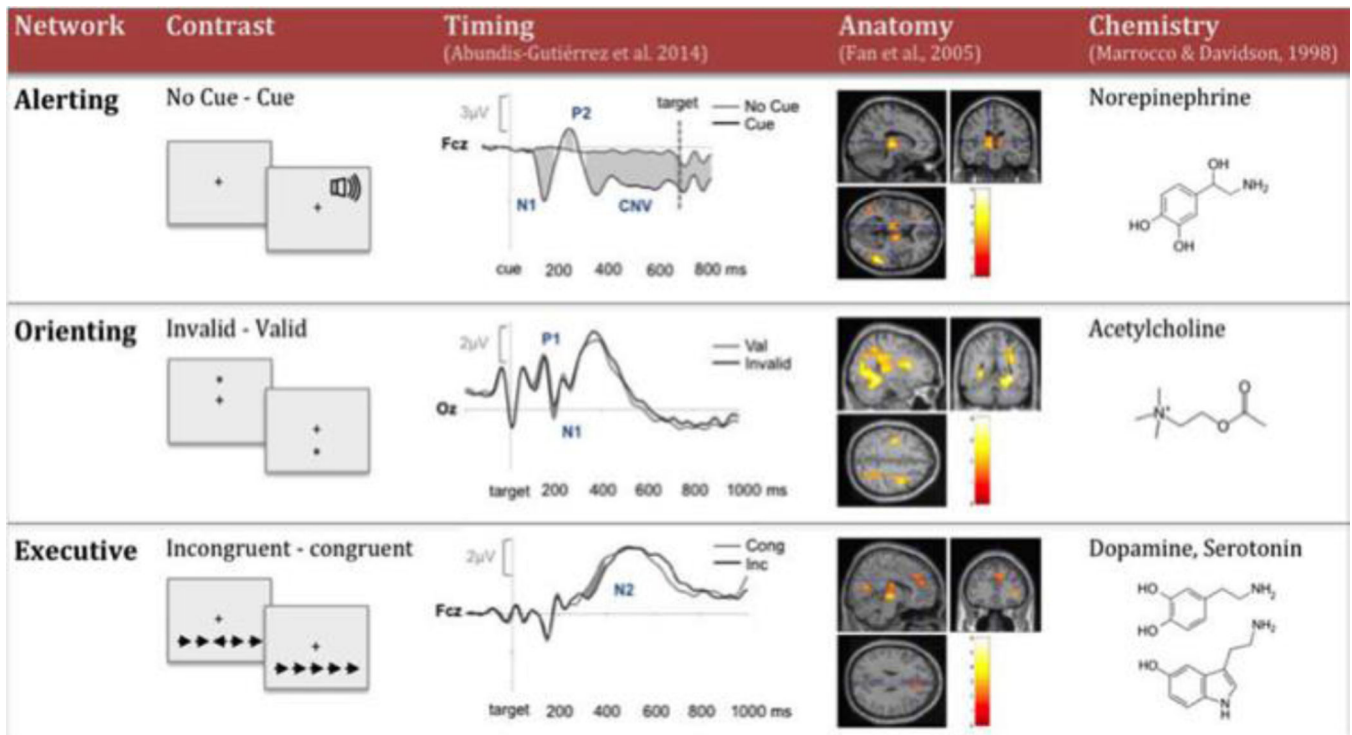


Figure 1. The Attention Network Test (ANT) is shown on the left of the figure
The test measures the efficiency of brain networks in children and adults by the speed of responding to whether a target stimulus points left or right. The bottom left column illustrates that the executive attention scores are calculated by the time to resolve conflict by subtracting the time to respond when all stimuli are in the same direction as the target from reaction time when incongruent stimuli are present. Alerting cues (top of column 1) indicate when the target will occur and orienting cues (middle of column 1) indicate where the target will occur. An alerting score is obtained by subtracting reaction times following a warning signal from those for unwarned trials. The orienting score is obtained from subtracting reaction times from trials indicating the target location from those without an orienting cue. The alerting, orienting and executive scores are related to the time course of brain activity by EEG (column 2), to the location of activation by fMRI (Column 3) and to chemical modulators (Column 4). Figure 1 is reprinted with permission from [1].