# Development of attentional networks

**Chapter** · January 2013

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CHAPTER

# 24

# Development of Attention Networks

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**Abstract**

Functions of attention include achievement and maintenance of a state of alertness, selection of information from sensory input, and regulation of responses when dominant or well-learned behavior is not appropriate. These functions have been associated with activation of separate networks of brain areas. We review the developmental course of the attention networks during infancy and childhood and the neural mechanisms underlying their maturation. Alerting is active early in infancy, although the ability to endogenously maintain the level of alertness develops through late childhood. The capacity to orient attention to external stimulation is also present from quite early in life, and most aspects of orienting related to the control of disengagement and voluntary orientation improve during childhood. Executive attention starts developing by the second half of the first year of life, showing significant maturation during the preschool years. The efficiency of all three functions is subject to important individual differences, which may be partially due to variations in genes related to neurotransmitters that modulate the activation of the attention networks. Additionally, attention can be fostered by training, and attention training has the potential to benefit aspects of behavior central to education and socialization processes. Finally, we discuss changes in attention that occur late in life.

**Key Words:** attention; development; attention networks; alerting; orienting; executive attention; infancy; childhood; individual differences; neurocognitive development

## Key Points

1. Functions of attention include maintenance of the alert state, orienting to sensory events, and self-regulation of responses.

2. The functions of attention are related to activation of separate networks of brain areas, named the alerting network, the orienting network and the executive attention network (see Fig. 24.1).

3. Viewing attention as an organ system with its own functional anatomy helps us to understand many complex issues related to development, including but not limited to (a) brain mechanisms underlying maturational processes, (b) constitutional factors that influence development, and (c) cognitive and brain mechanisms involved in attention-related pathologies.

4. Reaching the state of alertness from external cues can be done from early infancy. Further developments of the alerting network during childhood involve endogenous control of preparation and maintenance of the alert state.

5. Development of orienting appears to reach the adult level by mid childhood. Voluntary orienting and the control of disengagement of attention are aspects with a longer developmental course.

6. Executive attention is present from the second half of the first year of life and continues to develop throughout childhood, showing the most significant maturation during the preschool years.

7. Variations in genes related to neurotransmitters that modulate the activation

of the attention networks appear to influence the efficiency of the functioning of these networks in both adults and children.

8. Polymorphisms of particular attention-related genes (i.e., DRD4 and COMT) interact with environmental factors such as parenting. Interestingly, the polymorphisms of the DRD4 gene, associated with greater environmental influences, undergo positive selection in human evolution.

9. Attention can be improved through training. Attention training also improves fluid intelligence and may enhance regulation of affect as well.

10. Later-developing aspects of attention seem to be especially vulnerable to the influence of aging.

William James provided a good subjective description of attention as follows: "Everyone knows what attention is. It is the taking possession of the mind in clear and vivid form of one out of what seem several simultaneous objects or trains of thought." (James, 1890). However, this subjective definition does not provide hints that might lead to an understanding of attentional development or pathologies. We believe that viewing attention as an organ system with its own functional anatomy (Posner & Fan, 2008) can aid us in answering many complex issues related to development. Neuroimaging studies have systemically shown that a wide variety of cognitive tasks can be seen as activating a distributed set of neural areas, each of which can be identified with specific mental operations (Hillyard, Di Russo, & Martinez, 2006; Posner & Raichle, 1994; Posner, Rueda, & Kanske, 2007). Perhaps the areas of activation have been more consistent for the study of attention than for any other cognitive system (Raz & Buhle, 2006). Attention is therefore viewed as a system with networks of neural areas related to several major functions such as maintaining the alert state, orienting to sensory events, and the control of action in situations that involve conflict between responses.

In this chapter, we first review the anatomy of brain networks related to attention as revealed from imaging studies of adults. Then we consider how these networks develop during the first 2 years of life (infancy). We then consider what is known about how genes and experience interact during infancy. Next we examine the development of attention during childhood in the context of attentional functions in adults. We next discuss evidence for the ability to train attention at various stages of life.

Finally, we discuss changes in these networks that may appear late in life.

## Networks of Attention

Despite been viewed as a unitary system, attention has been associated to distinct functions related to the state of alertness, selectivity, and cognitive control (Broadbent, 1958; Kahneman, 1973; Posner, 1978; Norman & Shallice, 1986). While there have been many efforts to develop taxonomies of attention, imaging studies have suggested that three somewhat independent networks are involved in these different aspects of attention, carrying out the functions of alerting, orienting, and executive attention (Posner & Fan, 2008; Fig. 24.1). *Alerting* refers to achieving and maintaining a state of high sensitivity to incoming stimuli, *orienting* refers to the selection of information from sensory input, and *executive attention* includes mechanisms for monitoring and resolving conflict among thoughts, feelings, and responses.

The brain network involved in achieving and maintaining the alert state is represented with squares in Figure 24.1. Alertness is an important prerequisite for other attentional operations. Although we often contrast the alert state with sleep, just as sleep has various stages, so the degree of alertness also differs over time. The study of alertness often has involved changes in vigilance (tonic alertness) over the course of a task (Mackworth, 1969). Another approach to varying alertness is to provide a warning interval prior to the start of a task. Warning signals provide a phasic change in the level of alertness over millisecond intervals. This change involves widespread variation in autonomic signals such as heart rate (Kahneman, 1973) and cortical changes—for example, a negative shift in the scalp-recorded EEG called the contingent negative variation (Walter, 1964).

Much of attention research involves orienting to sensory events. The ease with which the experimenter can control the presentation of visual and auditory stimuli probably accounts for the popularity of studying orienting in different organisms and ages. Precisely controlling the presentation of stimulation also allows studying overt and covert forms of orientation. Overt orienting involves eyes and/or head movements toward the source of stimulation and usually occurs when sufficient time is allowed between the presentation of an orienting cue and the target. Covert orienting involves only orientation of attention and can be studied when not enough time is allowed to move the eyes and/or
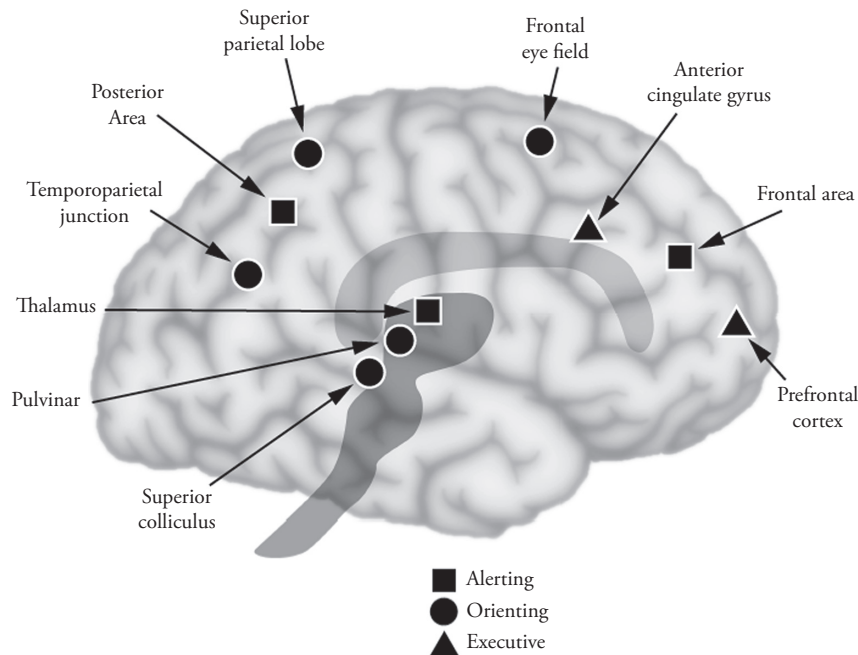
**Figure 24.1.** Anatomy of three attentional networks: Alerting, squares; Orienting, circles; Executive attention, triangles. (From Posner & Rothbart, 2007.)

head or by instructing individuals to attend to the cue without looking at it. Neuroimaging has shown that the neural systems underlying overt and covert attention in adults heavily overlap (Corbetta & Shulman, 2002). This system includes both parietal (temporal-parietal junction and superior parietal lobe) and frontal cortical areas (frontal eye fields) as well as some subcortical areas, including the superior colliculus and pulvinar. Imaging research has suggested that the temporal-parietal junction is most important for interrupting the current focus of attention, while the superior parietal lobe is more involved in voluntary movements of attention.

Every sensory signal provides input both to sensory specific cortical pathways and to brainstem arousal systems related to alerting. Together these signals may yield changes in a brain network of parietal and frontal areas (circles in Fig. 24.1) that orchestrate covert shifts of attention. This orienting network acts so as to boost the strength of input signals in sensory-specific pathways in comparison to nonattended signals.

Another aspect of attention, especially prominent in the transition between infancy and early childhood, is executive control and self-regulation. In daily life situations, responses are subject to greater or lesser degrees of conscious and/or volitional control. However, resources for the control of action are limited. In many models of cognitive control, monitoring and distributing resources have been attributed to a central control system related to attention (Kahneman, 1973; Norman & Shallice, 1986; Meyer & Kieras, 1997). A mechanism for attentive control of action is required when well-learned or automated behavior is not adequate to produce a desired response. According to Norman and Shallice (1986), situations that require attentional control are those involving (1) novelty, (2) error correction or troubleshooting, (3) some degree of danger or difficulty, or (4) overcoming strong habitual responses or tendencies. Thus, executive control of attention refers to mechanisms that enable detection and resolution of conflict between opposed activations (e.g., opposed response tendencies) by selection and commitment of resources (Posner & DiGirolamo, 1998; Posner & Petersen, 1990). The particular mechanisms involved in executive attention are monitoring, detection, and inhibition of processes and/or responses according to the goals of the individual (Rueda, Posner, & Rothbart, 2005). Effortful and voluntary control of attention is central to a broad range of abilities in executive function, such as planning, memory, and problem solving (see the chapter by Carlson et al. in this handbook). Therefore, there is an important overlap between executive attention and the broader concept of executive function,

which includes attentional control as well as activation and manipulation of memory representations. This overlap is often manifested by the use of similar experimental paradigms to study both executive attention and executive function.

There is evidence that effortful control is linked to a common brain network that is termed here the executive attention network (triangles in Fig. 24.1). The executive attention network is involved in the regulation of feelings (emotions), thoughts (cognitions), and actions (Posner & Rothbart, 2007). The anterior cingulate gyrus, one of the main nodes of the executive attention network, has been linked to a variety of specific functions related to self-regulation. These include the monitoring of conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001), control of working memory (Duncan et al., 2000), regulation of emotion (Bush, Luu, & Posner, 2000), and response to error (Holroyd & Coles, 2002). In emotional studies, the anterior cingulate is often seen as part of a network involving the orbital frontal cortex and the amygdala that regulates our emotional response to input. Activation of the anterior cingulate is observed when people are asked to control their natural reactions to strong positive (Beauregard, Levesque, & Bourgouin, 2001) or negative emotions (Ochsner, Bunge, Gross, & Gabrieli, 2002).

### The Attention Network Task (ANT)

Several years ago, Fan and colleagues (2002) developed an experimental task to study the functioning of the three attentional networks. The task is based on traditional experimental paradigms to study the functions of alerting (preparation cues), orienting (orienting cues), and executive control (flanker task). In the ANT, each trial starts with the presentation of a fixation cross. Then a cue consisting of an asterisk is presented on three quarters of the trials (in the other quarter of the trials no cue is presented). The cue can either have information about the upcoming of the target (alerting) but not of its location (double or central cue), or it could have both alerting plus orienting information (spatial cue). Finally, a target is presented consisting of an arrow pointing either right or left. The target, which appears either above or below the fixation cross, is flanked by two arrows on each side. The flanking arrows may point in the same direction as the target (congruent trials) or in the opposite direction (incongruent trials), equally often. In successive trials, participants are instructed to discriminate the direction of the target arrow by

pressing a corresponding key, left or right, in the computer's keyboard as rapidly and accurately as possible, while both reaction time (RT) and accuracy of the response are registered. Completion of the task allows calculation of three scores related to the efficiency of the attention networks. The *alerting score* is calculated by subtracting RT to trials with double cue to trials with no cue. This provides a measure of the benefit in performance by having a signal that informs about the immediate upcoming of the target and using this information to get ready to respond. The *orienting score* provides a measure of how much benefit is obtained in responding when information is given about the location of the upcoming target. It is calculated by subtracting RT to spatial cue trials from that of central cue trials. Finally, the *executive attention score* indicates the amount of interference experienced in performing the task when stimulation conflicting with the target is presented in the display. It is calculated by subtracting RT to congruent trials from RT to incongruent trials. Larger scores indicate more interference from distractors and therefore less efficiency of conflict resolution mechanisms (executive attention).

We have also developed a child-friendly version of the ANT (Rueda, Fan, McCandliss, Halparin, Gruber, et al., 2004a; Fig. 24.2). This version is structurally similar to the adult version but uses fish instead of arrows as target stimuli. This allows contextualization of the task in a game in which the goal is to feed the middle fish (target) by pressing a key corresponding to the direction of its mouth. After the response is made, the child version of the task provides feedback consisting of an animation of the middle fish. This is intended to help children's motivation to complete the task.

Each of the functions of attention considered in the neurocognitive model just described is present to some degree in infancy, but each undergoes a long developmental process. We trace the development of these functions in the next sections.

### Infancy

Attention in infancy is less developed than later in life, and the functions of alerting, orienting, and executive control in particular are less independent during infancy. However, we will first examine alerting and orienting and then consider attention in relation to self-regulation. The measurement of these variables must be different in infancy than later, when voluntary responses can be directed by the experimenter. Efforts have been made to design
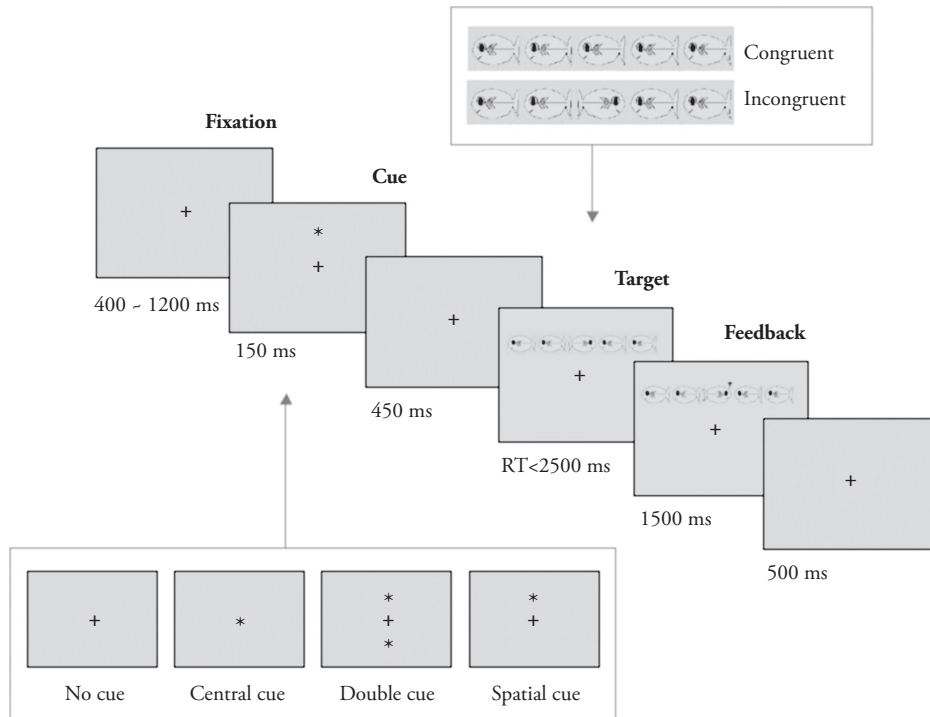
**Figure 24.2.** Schematic representation of the child version of the ANT.

tasks that can be performed by infants and tap the same networks of brain areas shown in Figure 24.1.

The early life of the infant is concerned with changes in state. Sleep dominates at birth and the waking state is relatively rare at first. The newborn infant spends nearly 75% of the time sleeping at birth (Colombo & Horowitz, 1987). Many of the changes in the alert state depend upon external input. Arousal of the central nervous system involves input from brainstem systems that modulate activation of the cortex. Primary among these is the locus coeruleus, the source of the brain's norepinephrine. It has been demonstrated that the influence of warning signals operates via this brain system, since drugs that block it also prevent the changes in the alert state that lead to improved performance after a warning signal is provided (Marrocco & Davidson, 1998). It is likely that the endogenous changes during waking that take place without external input also involve this system.

There is a dramatic change in the percentage of time in the waking state over the first 3 months of life. By the 12th postnatal week the infant has become able to maintain the alert state during much of the daytime hours. This ability still depends heavily upon external sensory stimulation, much of it provided by the caregiver.

Much of the response to external stimuli involves orienting toward a stimulus. Newborns show head and eye movement toward novel stimuli. These eye movements are preferentially directed toward moving stimuli and have been shown to depend upon properties of the stimulus—for example, how much they resemble human faces (Johnson & Morton, 1991). It has also been demonstrated that newborns can make imitative responses; when shown, for example, a face with a protruding tongue they respond with a similar movement (Meltzoff & Moore, 1977). However, the reliability and complexity of these responses to sensory input change dramatically over the first few months of life.

The most frequent method of studying orienting in infancy involves the use of tracking of saccadic eye movements. As in adults, there is a close relation between the direction of gaze and the infant's attention. The attention system can be driven by external input from birth (Richards & Hunter, 1998), but the system continues to improve in precision over many years. Infants' eye movements often fall short of the target, and peripheral targets are often foveated by a series of head and eye movements. Although not as easy to track, the covert system likely follows a similar trajectory. Studies that have attempted to examine the covert system by use of

brief cues that do not produce an eye movement, followed by targets that do, show that the speed of the eye movement to the target is enhanced by the cue, and this enhancement improves over the first year of life (Butcher, 2000). In more complex situations—for example, when there are competing targets—the improvement may go on for longer periods (Enns & Cameron, 1987).

Orienting to sensory input is a major mechanism for regulation of distress. Infants often have a hard time disengaging from high-spatial-frequency targets and might become distressed before they are able to move away from the target. Caregivers provide a hint of how attention is used to regulate the state of the infant when they attempt to distract infants by bringing their attention to other stimuli. As infants orient, they are often quieted, and their distress appears to diminish. In one study, 3- to 6-month-old infants (Harman, Rothbart, & Posner 1997) were first shown a sound and light display; about 50% of the infants became distressed to the stimulation, but then strongly oriented to interesting visual and auditory soothing events when these were presented. While the infants oriented, facial and vocal signs of distress disappeared. However, as soon as the orienting stopped (e.g., when the object was removed), the infants' distress returned to almost exactly the levels shown prior to presentation of the soothing object. An internal system, which we termed the *distress keeper*, and which we believe involves the amygdala, appears to hold a computation of the initial level of distress, so that this initial level returns if the infant's orientation to the novel event is lost. Interestingly, infants were quieted by distraction for as long as 1 minute without changing the eventual level of distress reached once orienting ended (Harman et al., 1997).

For newborn infants, the control of orienting is initially largely in the hands of caregivers. By 4 months, however, infants have gained considerable control over disengaging their gaze from one visual location and moving it to another, and greater orienting skill in the laboratory is associated with lower temperamental negative emotion and greater soothability as reported by parents (Johnson, Posner, & Rothbart, 1991). Late infancy is the time when self-regulation develops. Increasingly, infants are able to gain control of their own emotions and other behaviors. This transition marks the development of the executive attention system.

It is difficult to assess executive attention in infants because, as outlined above, caregivers provide most of the regulation of infant behavior. Effortful control is a high-level factor from parental reports (Rothbart & Rueda, 2005). This factor is defined as the ability to withhold a dominant response in order to carry out a nondominant one. Parents observing their children's behavior in particular daily life situations (e.g., putting away toys on command, etc.) can readily rate questions that relate to this factor. This can be done for children about 2 years of age on. Below this age, the Infant Behavior Questionnaire (Rothbart, Ahadi, & Hershey, 1994) is confined to factors such as orienting and positive and negative affect. Moreover, children above age 2 can be scored on tasks that involve voluntary responding, such as pressing keys to visual input.

Perhaps the earliest evidence of the executive attention network is at about 7 months. One study examined the ability of infants of 7 months to detect errors (Berger, Tsur, & Posner, 2006). In this study, infants observed a scenario in which one or two puppets were hidden behind a screen. A hand was seen to reach behind the screen and either add or remove a puppet. When the screen was removed, there was either the correct number of puppets or an incorrect number. Wynn (1992) found that infants of 7 months looked longer when the number was in error than when it was correct. Whether the increased looking time involved the same executive attention circuitry that is active in adults when they detect errors was simply unknown. Berger replicated the Wynn study but used 128-channel EEG to determine the brain activity that occurred during error trials in comparison with that found when the infant viewed a correct solution. In adults, a potential, named error-related negativity (ERN), appears some time (usually between 60 and 120 ms) after committing an error (Gehring, Gross, Coles, Meyer, & Donchin, 1993). This potential has a frontocentral scalp distribution, and analyses of the topography with source localization methods has suggested that the potential is generated at the anterior cingulate gyrus (Dehaene, Posner, & Tucker, 1994; van Veen & Carter, 2002). Berger and colleagues found that the same EEG component over the same electrode sites differed between correct and erroneous displays both in infants and adults. This suggests that a similar brain anatomy as in adult studies is involved in infants' ability to detect errors. Of course, activating this anatomy for observing an error is not the same as found in adults, who actually slow down after an error and adjust their performance. However, it suggests that even very early in life, the anatomy of the executive attention system is at least partly in place.

Later in the first year of life, there is evidence of further development of executive functions, which may depend upon executive attention. One example is Adele Diamond's work using the "A-not-B" task and the reaching task. These two marker tasks involve inhibition of an action that is strongly elicited by the situation. In the "A-not-B" task, the experimenter shifts the location of a hidden object from location A to location B, after the infant's retrieving from location A had been reinforced as correct in the previous trials (Diamond, 1991). In the reaching task, visual information about the correct route to a toy is put in conflict with the cues that normally guide reaching. A toy is placed under a transparent box. The opening of the box is on the side (it can be the front side, the back side, etc.), and the infant can reach it only if the tendency to reach directly along the line of sight through the transparent top of the box is inhibited. Important changes in the performance of these tasks are observed from 6 to 12 months (Diamond, 2006). Comparison of performance between monkeys with brain lesions and human infants on the same marker tasks suggests that the tasks are sensitive to the development of the prefrontal cortex, and maturation of this brain area seems to be critical for the development of this form of inhibition.

Another task that reflects the executive system involves anticipatory looking in a visual sequence task (Haith, Hazan, & Goodman, 1988). In the visual sequence task, stimuli are placed in front of the infant in a fixed and predictable sequence of locations. The infant's eyes are drawn reflexively to the stimuli because they are designed to be attractive and interesting. After a few trials, some infants will begin to anticipate the location of the next target by correctly moving their eyes in anticipation of the target. We have supposed that these anticipatory looks reflect the development of a more voluntary system that might depend in part upon the orienting network and also upon the early development of the executive network. It has been shown that anticipatory looking occurs with infants as young as 3.5 to 4 months (Clohessy, Posner, & Rothbart, 2001; Haith, Hazan, & Goodman 1988). However, there are also important developments that occur during infancy (Pelphrey, Reznick, Goldman, Sasson, Morrow, et al., 2004) and later (Garon, Bryson, & Smith, 2008). Learning more complex sequences of stimuli, such as sequences in which a location is followed by one of two or more different locations, the particular location depending on the location of the previous stimulus within the

sequence (e.g., 121312 …), requires the monitoring of context and, in adult studies, has been shown to depend on lateral prefrontal cortex (Keele, Ivry, Mayr, Hazeltine, & Heuer, 2003). We found that infants of 4 months do not learn to go to locations where there is conflict as to which location is the correct one. The ability to respond when such conflict occurs is not present until about 18 to 24 months of age (Clohessy et al., 2001). At 3 years, the ability to respond correctly when there is conflict in the sequential looking task correlates with the ability to resolve conflict in a spatial conflict task (Rothbart, Ellis, Rueda, & Posner, 2003). These findings support the slow development of the executive attention network during the first and second year of life.

The visual sequence task is related to other features that reflect executive attention. One of these is the cautious reach toward novel toys. Rothbart and colleagues found that the slow cautious reach of infants of 10 months predicted higher levels of effortful control as measured by parent report at 7 years of age (Rothbart, Ahadi, Hershey, & Fisher, 2001). Infants of 7 months who show higher levels of correct anticipatory looking in the visual sequence task also show longer inspection before reaching toward novel objects and slower reaching toward the object (Sheese, Rothbart, Posner, White, & Fraundorf, 2008). This suggests that successful anticipatory looking at 7 months is one feature of self-regulation. In addition, infants with higher levels of correct anticipatory looking also showed evidence for higher levels of emotionality in a distressing task and more evidence of efforts to self-regulate their emotional reactions. Thus, even at 7 months the executive attention system is showing some properties of self-regulation, even though it is not yet sufficiently developed to resolve the simple conflicts used in the visual sequence task or the task of reaching away from the line of sight in the transparent box task (Diamond, 1991).

An important question about early development of executive attention is its relation to the orienting network (see Fig. 24.1). Recall that the orienting network develops very early and has a critical role in regulation of emotion by the caregiver as early as 4 months. It was also found that orienting as measured from the Infant Behavior Questionnaire at 7 months was not correlated with effortful control as measured in the same infants at 2 years (Sheese, Voelker, Posner, & Rothbart, 2009). However orienting did show some relation with early regulation of emotional responding of the infants. Orienting was positively related to positive affect and negatively

related to negative affect. It was expected that orienting would be positively related to positive affect because previous work had shown that duration of orienting as reported by caregivers was longer for children higher in smiling and laughter. It was also expected that orienting would be negatively related to negative affect during infancy, given its use as a tool for soothing infants (Harman, Rothbart, & Posner, 1997).

By 2 years of age parents can give reports that lead to a measure of effortful control. Two-years-olds, however, did not show the usual pattern of negative relationships between effortful control and negative affect that has been repeatedly found at other ages (Rothbart & Rueda, 2005). This was unexpected, and it is possible that toddlers may be at a transition stage between emotional control by orienting and control by executive attention.

Colombo (2001) presented a summary of attentional functions in infancy, which included alertness, spatial orienting, object-oriented attention, and endogenous attention. This division is similar to the network approach, but it divides orienting into space and features and includes the functions of interstimulus shifts and sustained attention as part of endogenous attention. He argues that alerting reaches the mature state at about 4 months, orienting by 6 to 7 months, and endogenous attention by 4 to 5 years. This schedule is similar to our discussion in order, but as discussed in the next major section, all these functions continue developing during childhood. The genetic findings discussed below are new since the Colombo summary and add additional substance to the distinctions among functions and their integration in the achievement of self-regulation.

The findings to date suggest that orienting is playing some of the regulatory roles in early infancy that are later exercised by the executive network. Despite the common roles that orienting and executive networks play in regulating emotion, it is not clear whether orienting and its use by parents is important in the development of the executive attention. We consider this issue again later in the chapter as we examine the genes that relate to these early individual differences.

## Network Changes in Childhood
### Alerting Network

As discussed earlier, the state of alertness can be elicited by external stimulation or can be attained in a voluntary endogenously generated way. Young infants are able to attain the alert state when elicited by external stimulation, with a progressive increase in the frequency and duration of alert periods during the first year of life, whereas the ability to voluntary deploy attention seems to emerge later and shows a more steady developmental course along childhood (Colombo, 2001).

Preparation from warning cues (phasic alertness) can be measured by comparing the speed and accuracy of response to stimulation with and without warning signals (Posner, 2008). Presentation of warning cues prior to targets allows the individual to get ready to respond by increasing the state of alertness. This commonly results in increased response speed, although it may also cause declines in the accuracy of the response, particularly at short intervals between the warning cue and the target (Morrison, 1982; Posner, 1978).

The difficulty of using RT tasks with very young children makes studying developmental differences in preparation from alerting cues more challenging, yet several studies have examined developmental changes in phasic alertness between preschoolers, older children, and adults. Using the child ANT, Mezzacappa (2004) observed a trend to larger alerting scores (difference between RT in trials with and without warning cues) with age in a sample of 5- to 7-year-old children. Increasing age was associated with larger reductions in RT in response to warning cues. Older children also showed lower rates of omissions overall, which indicates a greater ability to remain vigilant during the task period. Moreover, young children (5-year-olds) appear to need more time than older children (8-year-olds) and adults to get full benefit from a warning cue, and they also seem to be less able to sustain the optimal level of alertness over time (Berger, Jones, Rothbart, & Posner, 2000; Morrison, 1982). The difficulty of maintaining the alert state without a cue is also observed for older children (10-year-olds) when compared to adults (Rueda, Fan, McCandliss, Halparin, et al., 2004a), suggesting that tonic or sustained attention continues developing through late childhood.

Sustained attention is frequently measured by examining variations in performance in a task along a relatively extended period of time, as in the so-called Continuous Performance Tasks (CPT). Variations in the level of alertness can be observed by examining the percentage of correct and/or omitted responses to targets or through indexes of perceptual sensitivity ($d'$) over time. With young children, the percentage of individuals who are able to complete the task can also be indicative of maturational

differences in the ability to sustain attention. In a study conducted with preschoolers, only 30% to 50% of the 3- to 4-year-olds were able to complete the task, whereas the percentage rose to 70% for 4- to 4.5-year-olds and close to 100% from that age up (Levy, 1980). Danis and colleagues (2008) found considerable increases in the ability to maintain and regain attention after a distraction period in a CPT between 2.5 and 3.5 years of age, and more consistent control of attention after age 4.5. However, even though the largest development of vigilance seems to occur during the preschool period, children continue to show larger declines in performance in CPT over time compared to adults through middle and late childhood, especially under more difficult task conditions. For instance, 7- to 9-year-old children show a larger decline in sensitivity (*d'*) and hits over time compared to adults in an auditory version of the CPT thought to be more challenging than the visual version of the task (Curtindale, Laurie-Rose, Bennett-Murphy, & Hull, 2007). Likewise, while performing a CPT with degraded stimuli, a steady increase of *d'* and rate of hits with age has been observed, reaching the adult level by around age 13 (Lin, Hsiao, & Chen, 1999).

Developmental changes in alertness during childhood and early adolescence appear to relate to continuous maturation of frontal systems during this period. One way to examine brain mechanisms underlying changes in alertness is by registering patterns of brain-generated electrical activation through electrodes placed on the scalp while warning cues are processed. Typically, several hundred milliseconds after a cue that predicts the upcoming occurrence of a target stimulus is presented, a negative variation of brain activity is generated up until the target appears (Walter et al., 1964). This electrophysiological index is called the *contingent negative variation* (CNV) and appears to be related to a source of activation in the right ventral and medial frontal areas of the brain (Segalowitz & Davies, 2004). In adolescents as well as adults, the CNV has been shown to relate to performance in various measures of intelligence and executive functions as well as functional capacity of the frontal cortex (Segalowitz, Unsal, & Dywan, 1992). Various studies have shown that the amplitude of the CNV increases with age, especially during middle childhood. For instance, Jonkman (2006) found that the CNV amplitude is significantly smaller for 6- to 7-year-old children compared to adults, but no differences were observed between 9- to 10-year-olds and adults (Jonkman, 2006). Moreover, the difference in CNV amplitude

between children and adults seems to be restricted to early components of the CNV observed over right frontocentral channels (Jonkman, Lansbergen, & Stauder, 2003), which suggests a role of maturation of the frontal alerting network.

### Orienting Network

Babies are able to orient attention to external stimulation. Nonetheless, aspects of the attention system that increase precision and voluntary control of orienting continue developing throughout childhood and adolescence. Most infant studies examine overt forms of orienting. By the time children are able to follow instructions and respond to stimulation by pressing keys, both overt and covert orienting can be measured. The cuing task developed by Posner (1980) has been widely used to study the development of visual orienting along the lifespan. In this task, a cue is displayed prior to the presentation of a target to which a response, usually a key press, is required. The cue is aimed to induce orientation of attention to a particular location, and the target may appear at the cued location or at an uncued one. Then, particular operations involved in orienting of attention can be studied. When the target appears at the cued location, benefits of orienting attention to that location in the RT and accuracy of response to the target can be measured. When the cue is presented at a location different from the target, a cost in RT is observed that is thought to be due to operations of disengagement of attention from the cued location and reorientation to the location occupied by the target. Imaging research and studies carried out with patients have provided information on the brain anatomy related to each of these orienting operations (see Posner & Fan, 2008; Posner, Rueda, & Kanske, 2007). For instance, endogenous (voluntary) orientation of attention is associated with structures of the superior parietal lobe and the frontal eye fields, whereas exogenous (automatic) orienting seems to be the function of a network comprising the temporoparietal junction and ventral frontal cortex, largely lateralized to the right hemisphere (Corbetta & Shulman, 2002). Activation of these cortical areas is required for disengaging from the current focus of attention. Moving attention from one location to another involves the superior colliculus, whereas engaging attention requires thalamic areas such as the pulvinar nucleus.

Mostly using Posner's cuing paradigm, several studies have examined the development of orienting during childhood. Despite a progressive increase

in orienting speed to valid cues during childhood (Schul, Townsend, & Stiles, 2003), data generally show no age differences in the orienting benefit effect between young children (5 and 6 years of age), older children (8 to 10), and adults (Enns & Brodeur, 1989), regardless of whether the effect is measured in covert or overt orienting conditions (Wainwright & Bryson, 2002). However, there seems to be an age-related decrease in the orienting cost (Enns & Brodeur, 1989; Schul et al., 2003; Wainwright & Bryson, 2002). Besides, the effect of age when disengagement and reorienting to an uncued location is needed appears to be larger under endogenous orienting conditions (e.g., longer intervals between cue and target) (Schul et al., 2003; Wainwright & Bryson, 2005). This suggests that mostly aspects of orienting related with the control of disengagement and voluntary orientation, which depend on cortical regions of the parietal and temporal lobes, improve with age during childhood. In a study in which endogenous orienting was examined for children aged 6 to 14 and adults, all groups but the youngest children showed larger orienting effects, calculated as the difference in RT to targets appearing at cued and uncued locations, with longer cue–target intervals (Wainwright & Bryson, 2005). This indicates that young children seem to have problems endogenously adjusting the scope of their attentional focus. This idea was also suggested by Enns and Girgus (1985), who found that attentional focusing as well as the ability to effectively divide or switch attention between stimuli improves with age between ages 5, 8, and 10 years, and adulthood.

### Executive Attention Network

Self-regulation of cognition and action can be measured in the laboratory by registering responses to tasks that involve conflict. Common conflict tasks, like the classic Stroop task, require the participant to avoid paying attention to aspects of the stimulation (e.g., the word *WHITE*) that may be dominant (i.e., semantic information contained in the word) while responding to nondominant features (i.e., the color in which the word is written). From 2 years of age and older, children are able to perform simple conflict tasks in which their RT can be measured. The Spatial Conflict task (Gerardi-Caulton, 2000) induces conflict between the identity and the location of an object. In this task, pictures of houses of two animals (i.e., a duck and a cat) are presented in the bottom left and right sides of the screen, then one of the two animals appears either on the left or right side of the screen in each trial and the child

is required to show the animal what its house is by touching it. Location is the dominant aspect of the stimulus, although instructions require responding according to its identity. Thus, conflict trials in which the animal appears on the side of the screen opposite to its house usually cause slower responses and larger error rates than nonconflict (when the animal appears on the side of its house) trials. Between 2 and 4 years of age, children progressed from an almost complete inability to carry out the task to relatively good performance. Although 2-year-old children tended to perseverate on a single response, 3 year-olds performed at high accuracy levels, although, like adults, they responded more slowly and with reduced accuracy to conflict trials (Gerardi-Caulton, 2000; Rothbart, Ellis, Rueda, & Posner, 2003).

The detection and correction of errors is another form of action monitoring. While performing the Spatial Conflict task, 2.5- and 3-year-old children showed longer RTs following erroneous trials than following correct ones, indicating that children were noticing their errors and using them to guide performance in the next trial. However, no evidence of slowing following an error was found at 2 years of age (Rothbart et al., 2003). A similar result with a different timeframe was found when using a version of the Simple Simon game. In this task, children are asked to execute a response when a command is given by one stuffed animal, while inhibiting responses commanded by a second animal (Jones, Rothbart, & Posner, 2003). Children of 36 to 38 months were unable to inhibit their response and showed no slowing following an error, but at 39 to 41 months, children showed both an ability to inhibit and a slowing of reaction time following an error. These results suggest that between 30 and 39 months children greatly develop their ability to correct behavior based on erroneous responses, even though the basic process of error detection may occur as early as 7 months (Berger, Tzur, Posner, 2006) as was suggested previously.

The development of executive attention has also been traced into the primary-school period (Rueda et al., 2004a) using the child version of the ANT. Overall, children's reaction times were much longer than adults', but considerable development in the speed of resolving conflict from age 4 to about 7 years of age was observed. However, the ability to resolve conflict on the flanker task, as measured by increases in RT and percentage of errors produced by the presence of incompatible compared to compatible flankers, remained about the same from age

7 to adulthood. Nonetheless, studies in which the difficulty of the conflict task is increased by other demands such as switching rules or holding more information in working memory have shown further development of conflict resolution between late childhood and adulthood. For example, Davidson and colleagues (2006) manipulated (1) memory load, (2) inhibitory demand, and (3) rule switching (cognitive flexibility) in a Spatial Conflict (Simon) task. They found that the cost due to the need for inhibitory control was larger for children compared to adults. Also, even under low memory load conditions, the switching cost was still larger for 13-year-old children compared to adults (Davidson, Amso, Anderson, & Diamond, 2006). The longer developmental course observed with this task might be due to the requirement of additional frontal brain areas to those involved in executive attention. It is also possible that the development of executive attention continues well beyond the age of 7 to 8 years when conflict resolution times are stable as measured by the ANT.

To study the brain mechanisms that underlie the development of executive attention, some developmental studies have been carried out using event-related potentials (ERP) and conflict tasks. In one of these studies, a flanker task was used to compare conflict resolution in three groups of children aged 5 and 6, 7 to 9, and 10 to 12, and a group of adults (Ridderinkhof & van der Molen, 1995). In this study, developmental differences were examined in two ERP components, one related to response preparation (LRP) and another one related to stimulus evaluation (P3). The authors found differences between children and adults in the latency of the LRP, but not in the latency of the P3 peak, suggesting that developmental differences in the ability to resist interference are mainly related to response competition and inhibition, but not to stimulus evaluation.

As discussed earlier, brain responses to errors are also informative of the function of the executive attention system. The amplitude of the ERN seems to reflect detection of the error as well as salience of the error for a particular individual in the context of the task and therefore is subject to individual differences in affective style or motivation. Generally, larger ERN amplitudes are associated with greater engagement in the task and/or greater efficiency of the error-detection system (Santesso, Segalowitz, & Schmidt, 2005; Tucker, Hartry-Speiser, McDougal, Luu, & deGrandpre, 1999). Developmentally, the amplitude of the ERN shows a progressive increase

during childhood into late adolescence (Segalowitz & Davies, 2004), with young children (age 7 and 8 years) being less likely to show the ERN to errors than older children and adults—at least in the flanker task. This may reflect the progressive maturation of the brain system for action monitoring and regulation.

Another evoked potential, the N2, has been related to situations that require executive control (Koop, Rist, & Mattler, 1996), such as Go/No Go and flanker tasks. Efforts using algorithms designed to localize the source of the potential suggest that it is associated with activation coming from the anterior cingulate cortex (van Veen & Carter, 2002). We have conducted an ERP study in which we used the fish flanker task of the child ANT with 4-year-old children and adults (Rueda, Posner, Rothbart, & Davis-Stober, 2004b). Adults showed larger N2 for incongruent trials over the midfrontal leads. Four-year-old children also showed a larger negative deflection for the incongruent condition compared to the congruent one at the midfrontal electrodes. Compared to adults, this congruency effect had a larger size and extended over a longer period of time. Whereas the frontal effect was evident for adults at around 300 ms after the target, children did not show any effect until approximately 550 ms after the target. In addition, the effect was sustained over a period of 500 ms before the children's responses, in contrast with only 50 ms in the case of adults. Another important difference between 4-year-old children and adults was the distribution of effects over the scalp. In adults, the frontal effects appear to be focalized on the midline, whereas in children the effects were observed mostly at prefrontal sites and in a broader number of channels, including midline and lateral areas. Later in childhood, developmental studies have shown a progressive decrease in the amplitude and latency of the N2 effect with age (Davis, Bruce, Snyder, & Nelson, 2003; Johnstone, Pleffer, Barry, Clarke, & Smith, 2005; Jonkman, 2006). The reduction of the amplitude appears to relate to the increase in efficiency of the system, independently of age (Lamm et al., 2006). Also, the effects are more widely distributed for young children and they become more focalized with age (Jonkman, 2006). Source localization analyses indicate that, compared to adults, children need additional activations to adequately explain the distribution (Jonkman, Sniedt, & Kemmer, 2007).

The focalization of signals in adults as compared to children is consistent with neuroimaging studies conducted with older children, where children

appear to activate the same network of areas as adults when performing similar tasks, but the average volume of activation appears to be remarkably greater in children compared to adults (Casey, Thomas, Davidson, Kunz, & Franzen, 2002; Durston et al., 2002). All together, these data suggest that the brain circuitry underlying executive functions becomes more focal and refined as it gains in efficiency. This maturational process involves not only greater anatomical specialization but also reducing the time these systems need to resolve each of the processes implicated in the task. This is consistent with recent data showing that the network of brain areas involved in attentional control shows increased segregation of short-range connections but increased integration of long-range connections with maturation (Fair et al., 2007). Segregation of short-range connectivity may be responsible for greater local specialization, whereas integration of long-range connectivity likely increases efficiency by improving coordinated responses between different processing modules.

### Individual Differences

The executive attention network, represented in Figure 24.1, is thought to be roughly common to all people (Mezzacappa, 2004) and appears to be active even in infancy. However, as discussed in the previous section, there are also marked individual differences in self-regulation.

The study of individual differences on emotional reactivity and self-regulation in childhood has been undertaken by temperament research (Rothbart & Bates, 2006). Temperament studies have shown that some children are more subject to overstimulation and negative emotion than others, and will therefore need to decrease stimulation, while other more exuberant and extraverted children will be seeking excitement (Rothbart & Bates, 2006). Children also differ in effortful control. Individual differences in effortful control are related to the ability of the child to resolve conflict and thus to the efficiency of the executive attention network (Rothbart & Rueda, 2005). However, fear also serves as a control system that operates before effortful control is fully developed.

#### *Fear as a Control System*

Late in the first year, some infants also begin to demonstrate fear in their inhibited approach to unfamiliar and intense stimuli (Rothbart, 1988; Schaffer, 1974), and fearful behavioral inhibition shows considerable longitudinal stability across

childhood and into adolescence (Kagan, 1998; see the chapter by Kagan in this handbook). Fearful inhibition developing late in the first year of life allows inhibitory control of behavior. In a longitudinal study it was found that infant fear assessed in the laboratory predicted childhood fear, sadness, and shyness at 7 years (Rothbart et al., 2001). Fear did not predict later frustration/anger, but was inversely related to later approach, impulsivity, and aggression. These findings suggest that fear is also involved in the self-regulation of approach-related and aggressive tendencies (Gray & McNaughton, 1996).

More fearful infants also appear to later show greater empathy, guilt, and shame in childhood (Rothbart, Ahadi, & Hershey, 1994). These findings suggest that fear might be involved in the early development of moral motivation. Kochanska (1995, 1997) has indeed found that temperamental fearfulness predicts the development of conscience, understood as the internalization and application of moral norms, in preschool-age children (see the chapter by Smetana in this handbook). On the other hand, extreme fear may lead to problems in children's rigid overcontrol of behavior, as reflected in the Blocks' description of inflexible patterns of response that can limit children's positive experiences (Block & Block, 1980; Kremen & Block, 1998). Thus, the temperamental dimension of fearfulness within the first year of life allows the first major control system of behavior, but it is a reactive one that can lack flexibility. During the toddler and preschool years, development of executive attention underlying effortful control allows the child greater control of stimulation and response, including the ability to select responses in a conflict situation. We later discuss this development.

#### *Genetic Variation*

Links between the cognitive processes supporting executive attention and the activation of particular brain areas and the neurochemical processes that modulate their functioning (Posner, Rueda, & Kanske, 2007) suggest that this function may have a genetic origin. Indeed, recent twin studies show very high heritability for all aspects of executive function (Friedman, Miyake, Young, DeFries, Corley, & Hewitt, 2008). Additionally, studies of effortful control reveal marked individual differences that are stable over relatively long periods. These individual differences could reflect genetic variation. A step toward understanding this genetic variation is to determine whether differences in genes are related

to individual differences in executive attention and effortful control.

Many studies on genetic influences on attention use adults as participants. For example, the ANT was used to examine individual differences in the efficiency of the executive network (Fan, McCandliss, Sommer, Raz, & Posner, 2002). Executive attention network scores were found to be reliable over repeated presentations. Since the executive attention network is modulated by input from dopamine-rich brain areas such as the ventral tegmental area, genes related to dopamine receptors and transporters were used as a means of searching for candidates that might relate to the efficiency of attentional networks (Fossella, Sommer, Fan, Wu, Swanson, Pfaff, & Posner, 2002). The dopamine receptor D4 gene was an obvious candidate because of its association with attention-deficit disorders (Swanson et al., 2000).

To carry out these studies, 200 persons performed the ANT and were genotyped to examine frequent polymorphisms in genes related to dopamine. There were significant associations of two genes, the *dopamine receptor D4* (DRD4) and the *monoamine oxidase A* (MAOA), with executive attention. In particular, the VNTR 4-repeat polymorphism at exon III of the DRD4 gene and the 3-repeat at the promoter repeat polymorphism of the MAOA gene were associated with greater efficiency of the executive attention network (Fossella et al., 2002). In a neuroimaging experiment, persons with alleles of these two genes associated with more efficient handling of conflict showed significantly more activation in the anterior cingulate, a major node of the executive attention network, while performing the ANT than those with the allele associated with poorer performance (Fan, Fossella, Sommer, Wu, & Posner, 2003).

Recent studies have extended these observations. In two different studies employing conflict-related tasks other than the ANT, alleles of the *catechol-o-methyl transferase* (COMT) gene were also found to be related to the ability to resolve conflict (Blasi, Mattay, Bertolino, Elvevåg, Callicott, et al., 2005; Diamond, Briand, Fossella, & Gehlbach, 2004). A study using the child ANT showed that children homozygous for the 10-repeat allele of the DAT1 gene showed smaller conflict scores than children with at least one 9-repeat allele (Rueda, Rothbart, McCandliss, Saccamannno, & Posner, 2005). There is also increasing evidence that people with different alleles of the serotonin genes, either alone or in interaction with dopamine, show differences in executive attention (Canli, Omura, Haas, Fallgatter, Todd, et al., 2005; Reuter, Ott, Vaidl, & Hennig, 2007).

There are also adult studies showing that genetic variations influencing the cholinergic system are related to individual differences in visual search tasks (Parasuraman, Greenwood, Kumar, & Fossella, 2005). Visual search can be rather complex and could draw upon both orienting and executive control, depending on the exact task used. Studies of monkeys suggest the importance of cholinergic input for the orienting network, and sometimes these have been used to argue that the findings for visual search relate primarily to the orienting network (Posner, Rothbart, & Sheese, 2007). This issue is still unsettled, however; new findings with infants (see below) suggest that at least some of the influence of cholinergic related genes may be upon the executive attention network. It is expected that genes influencing individual differences would also be genes that influence the developmental course of attentional networks. One step testing this idea is to see if the alleles known to influence adult attention would have similar effects in infants and young children. If there is continuity in the effects of genetic variation on individual differences in attention, one would have additional support for thinking of these genes as crucial to attentional development.

### Genes and Development

Seven-month-old infants with the T/T variation of the *cholinergic receptor, nicotinic, alpha-4* (CHRNA4) gene have a higher level of anticipations in the visual sequence task than those with the C/C allele (Sheese, Voelker, Posner, & Rothbart, 2009). In adults, Parasuraman and colleagues (2005) have shown that those with the T/T allele also have better orienting skills in a cued spatial attention task. Both of these findings support a role for the CHRNA4 gene in orienting of attention. This fits well with the link between the cholinergic system and orienting mechanisms of the parietal lobe.

Because many of the visual search tasks that Parasuraman found to be related to CHRNA4 involve elements of executive attention as well as orienting, it is not entirely clear whether only orienting or both networks are involved. Similarly, in 2-year-olds, CHRNA4 was related to parental reports of effortful control. However, this finding depended on the cuddliness subscale, which is less central to the executive attention network. Future research may help us understand whether CHRNA4 in infancy and childhood is related only

to orienting or whether it also plays a role in executive attention.

The 7-repeat allele of the DRD4 gene has been linked to attention-deficit/hyperactivity disorder (ADHD) and to the temperamental quality of risk taking (see the chapter by Sonuga-Barke in this handbook). Adults and children with the 7-repeat allele have been shown to be higher in the temperamental quality of risk taking and to have a high risk for attention-deficit disorder than those with smaller numbers of repeats (Auerbach, Benjamin, Faroy, Kahana, & Levine, 2001; Swanson et al., 2001). Also, in one series of studies (Auerbach et al., 1999), it was found that orienting of 2-month-old infants as rated by parents and observed during inspection of toys was related to the presence of the 7-repeat allele of the dopamine 4 receptor gene. This allele appears to interact with a gene related to serotonin transmission, 5HTT.

Evidence that environment and/or experience can have a stronger influence in individuals with the 7-repeat allele has been reported by Bakermans-Kranenburg and van Ijzendoorn (2006; van Ijzendoorn & Bakermans-Kranenburg, 2006). Moreover, in one study an intervention that increased parental use of positive discipline reduced externalizing behavior in toddlers with the 7-repeat allele of the DRD4 gene significantly more than for those without this allele (Bakersman-Krannenburg, IJzendoorn, Pijlman, Mesman, & Juffer, 2008). This finding is important because assignment to the intervention group was random, thus ensuring that the result is not due to something about the parents other than the training.

In a longitudinal study conducted at the University of Oregon, cheek swabs were used to extract DNA and determine the genetic variation in a dozen of the genes that had been connected to attention in adult studies (Sheese, Voelker, Rothbart, & Posner, 2007). These children had been seen when they were 7 months old, but the genotyping took place when they returned to the laboratory at about 2 years of age. In addition, parenting quality was examined through observation of caregiver–child interactions in which the children played with toys in the presence of one of their caregivers. Raters watched the caregiver–child interaction and rated the parents on five dimensions of parental quality according to a schedule developed by NICHD (1993): support, autonomy, stimulation, lack of hostility, and confidence in the child. According to their scores parents were divided at the mean into two groups: one showing a higher quality

of parenting, and the other a lower quality. Results showed an interaction between parenting quality and variation of the DRD4 gene. For children with the 7-repeat allele, there was a strong influence of parenting quality. Parents who were rated as giving greater support, autonomy, etc., had children who were close to average in the ratings of their parents of their impulsivity. However, children with the 7-repeat allele whose parents had shown lower-quality parenting were much higher in impulsivity. Children without the 7-repeat allele showed the same-rated impulsivity regardless of parenting, and their impulsivity did not differ from children with the 7-repeat allele who received higher-quality parenting. However, children with the 7-repeat allele whose parents had shown lower-quality parenting were much higher in impulsivity. Similar results were obtained for activity level and high-intensity stimulation seeking, which can be combined into one aggregate measure of risk taking.

Evidence shows that the 7-repeat allele is under positive selective pressure in recent human evolution (Ding, Chi, Grady, Morishima, Kidd, et al., 2002). Why should an allele related to ADHD be positively selected? We think that positive selection of the 7-repeat allele could well arise from its sensitivity to environmental influences. Parenting provides training for children in the values favored by the culture in which they live. For example, Rothbart and colleagues (Ahadi, Rothbart, & Ye, 1993) found that in Western culture effortful control appears to regulate negative affect (sadness and anger), while in China (at least in the1980s) it was found to regulate positive affect (outgoingness and enthusiasm). In recent years, the genetic part of the nature-by-nurture interaction has been given a lot of emphasis (see the chapters by Moore and Suomi in this handbook). Theories of positive selection in the DRD4 gene have stressed the role of sensation seeking in human evolution (Harpending & Cochran, 2002; Wang, Kodama, Baldi, & Moyzis, 2006). The finding that individual differences in impulsivity may be influenced by the interaction between genetics and parenting style do not contradict this emphasis, but suggest a form of explanation that could have even wider significance. If genetic variations are selected according to the sensitivity to cultural influences that they produce in children, this could support a greater balance between genes and environment. It remains to be seen whether the other 300 genes estimated to show positive selection would also increase an individual's sensitivity to variations in rearing environments.

AQ: The year is 2000 in the reference list, not 2001. which is correct?

AQ: please add "van Ijzendoorn & Bakermans-Kranenburg (2006)" to the reference list.

How could variation in genetic alleles lead to enhanced influence of cultural factors such as parenting? The anterior cingulate receives input pertaining to both reward value and pain or punishment, and this information is clearly important in regulating thoughts and feelings. Dopamine is the most important neuromodulator in these reward and punishment pathways. Thus, changes in the availability of dopamine could enhance the influence of signals from parents related to reward and punishment. Another interaction has been reported between the serotonin transporter and parental social support on the temperamental dimension of behavioral inhibition or social fear (Fox, Nichols, Henderson, Rubin, Schmidt, et al., 2005; see the chapter by Kagan in this handbook). To explain this interaction, Fox, Hane, and Pine (2007) argue that those children with a short form of the serotonin transporter gene who also have lower social support from parents show enhanced attention to threat and greater social fear. However, in the study by Sheese and colleagues (2007), data showed that there was no influence of the 7-repeat allele on executive attention; rather, the gene and environment interacted to influence the child's behavior as observed by his or her caregiver. However, the same children at age 4 did show an interaction between the presence of the DRD4 7-repeat allele and parenting quality in determining effortful control. Since effortful control is linked to executive attention, this finding suggests that the executive network could be a mechanism for the widespread effects of Gene x Environment interactions, at least in older children and adults. It is important to consider the multiple mechanisms by which genes may influence behavior. Clearly one important mechanism lies in the executive attention network we have been discussing in this chapter, but there must be other pathways that influence the same behavior.

Recent work has found another Gene x Environment interaction that works through attention. One of the strongest links between adult individual differences in attention and genes is for the COMT gene, which is also one of the genes undergoing positive selection (Ding et al., 2002). In most studies one genotype (Met-Met) shows better performance in a variety of tasks than does the other (Val-Val). Moreover, a study of 7- to 14-year-old children (Diamond et al., 2004) found a similar effect at this age. Another approach to the gene has been to construct a haplotype consisting of three different polymorphisms in the gene. Versions of this haplotype have been shown to be closely related to the perception of pain (Diatchenko et al., 2005). Executive attention and pain both have been shown to involve the anterior cingulate gyrus. In both 7-month-olds and 2-year-olds, both the genotype and the haplotypes proved to be related to aspects of performance in the visual sequence task (Voelker, Sheese, Rothbart, & Posner, 2009). Although the haplotype was more strongly linked to performance, it is not clear which of the two characterizations is best. At 2 years of age it was possible to examine the relation between parenting and variations in the COMT gene that were common to both genotype and haplotype. An interaction was found between the genetic variation and parenting quality in determining performance in the visual sequence task. In particular, those 2-year-olds with higher-quality parenting and the haplotype that included the Val-Val genotype were superior in the task (Voelker et al., 2009).

## Training Attention

The presence of large individual differences in attention right from infancy and the importance of environmental factors such as nutrition, socioeconomic status, and parenting for attentional function suggest that the ability of children to maintain, orient, and control attention may depend upon the joint interaction of genes and environment. The relation of genetic factors to the functioning of the executive attention system does not mean that the system cannot be influenced by experience. Indeed, the interaction between genes and environment discussed above suggests that sensitivity to the environment might be built into genetic variation. Several training-oriented programs have been successful in improving attention in patients suffering from different pathologies. For example, the use of Attention Process Training (APT) has led to specific improvements in executive attention in patients with specific brain injury (Sohlberg, McLaughlin, Pavese, Heidrich, & Posner, 2000) as well as in children with ADHD (Kerns, Eso, & Thomson, 1999). Work with ADHD children has also shown that working memory training can improve attention (Klingberg, Forssberg, & Westerberg, 2002; Olesen, Westerberg, & Klingberg, 2004). Moreover, training with videogames has been shown to produce better performance on a range of visual attention tasks in normal adults (Green & Bavelier, 2003, 2006).

Other studies have aimed at examining the role of experience on the attention system during normal development. In our laboratory we developed a training intervention that uses computerized

exercises and tested it during the period of major development of executive attention: between 4 and 7 years of age (Rueda, Posner, & Rothbart, 2005). The training consists of a set of training exercises structured in various levels of difficulty. Some exercises intend to train target tracking and anticipation (e.g., predict where a duck cartoon will come out given a particular trajectory that can be either visible or invisible). Matching-to-sample exercises train attentional focusing and discrimination as well as working memory in conditions where the sample object disappears during the response phase and therefore needs to be memorized. The program also includes Stroop-like exercises aimed at giving children practice in resolving conflict. Finally, some exercises target inhibitory abilities such as response control in Go/No Go situations and inhibition of perceptual interference (Rueda, Rothbart, Saccomanno, & Posner, 2007).

Using this training program, we have conducted several studies in which children who went through five 45-minute training sessions over a 2-week period were compared with a randomly selected control group who spend an equivalent time watching cartoon videos. Recording of brain activation during performance of the child ANT before and after training showed clear evidence of improvement in the executive attention network following training. We looked at the effect of training in a late positive component (LPC) of the ERP observed for young children over frontal channels, which appear to be modulated by conflict (Rueda et al., 2004b), as well as the N2. Compared to nontrained children, trained 4-year-olds showed the LPC several tens of milliseconds earlier (Rueda, Rothbart, McCandliss, Saccomanno, & Posner, 2005). Moreover, trained 6-year-olds showed N2 differences between congruent and incongruent conditions that resembled those found in adults while performing the child ANT (Rueda et al., 2004b) or other versions of the flanker task (Jonkman, Sniedt, & Kemner, 2007; van Veen & Carter, 2002). These data suggest that training altered the network for the resolution of conflict in the direction of being more like what is found in adults. We also found a significantly greater improvement in fluid intelligence as measured with the K-BIT (Kaufman & Kaufman, 1990) in the trained group compared to the control children (Rueda, Rothbart, McCandliss, et al., 2005). This finding suggested that training effects had generalized to a measure of cognitive processing different from the function targeted by the training exercises. It also suggests

that efficiency of the network related to IQ, which includes both medial and lateral frontal brain areas (Duncan et al., 2000), would also be improved, probably due to enhanced monitorization and distribution of attentional resources between relevant processes involved in the tasks after training of executive attention.

In a more recent study conducted in a Spanish preschool with a sample of 5-year-old children, we have replicated and extended the effects obtained with our training program (Rueda, Checa, & Cómbita, 2012). In this study, a follow-up session was given 2 months after the training. Again, the trained group showed a significant improvement in intelligence following training, and this improvement was maintained over the 2-month period without further training, while the control group did not show such improvement. In this study, source analyses of the recorded brain electrical activity showed that trained children compared to the control group showed an earlier and more efficient engagement of executive attention structures (e.g., dorsal anterior cingulate cortex) while performing the child ANT. Importantly, this advantage of the trained group was maintained in the follow-up assessment. Moreover, training of attention also produced modest beneficial effects on performance of tasks involving affective regulation, such as delay of reward (Prencipe & Zelazo, 2005) and regulation of wins and loses in a gambling task for children (Kerr & Zelazo, 2004).

The training in children seemed to work primarily on the executive attention network, which is closely associated with our feelings of effort. Improvement in this network could have widespread influence on behavior. For example, attentional difficulties are a very frequent symptom related to failure in school (Checa, Rodriguez-Bailon, & Rueda, 2008) and to different forms of psychopathology (Rothbart & Posner, 2006). However, without a real understanding of the neural substrates of attention, there have not been systematic efforts to remedy attentional problems. We find that the study of attention training as a whole suggests that networks can be improved by training. The results discussed above suggest that benefits of attention training may transfer to regulation in affectively relevant situations. This finding is consistent with the role given to the executive attention network in the regulation of both cognitive and affective processes. With a better understanding of which training method improves what aspect of the network function, it might be possible to design more appropriate methods for

children of various ages and with various forms of disabilities.

## Brain Connectivity and Lifespan Development

Many studies of attention involve young adults, often undergraduates. The three networks described above have been examined in behavioral and genetic studies, and these studies have been summarized in several papers (Posner & Fan 2008; Raz & Buhle, 2006). The infant and child studies described in this chapter have often been compared with the studies of young adults in attempting to understand what has been developing.

Of course, development does not end with young adults. There have been many studies documenting an increase in RT and a decrease in accuracy and a reduction of problem-solving ability and fluid intelligence in elderly persons compared to young adults (Salthouse, 2005). These are generally not longitudinal studies because of the years involved, and like all cross-sectional research they may be subject to bias in the selection of people at various ages. Despite this problem, the studies using modern imaging methods that have been carried out in elderly persons have provided some insight into changes that occur later in life that are closely related to the brain networks we have been examining (Andrew-Hana et al., 2007; Fair et al., 2008; Fernandez-Duque & Black, 2006; Pardo et al., 2007).

In one study, Pardo and colleagues (2007) used positron emission tomography (PET) to examine metabolism in 46 persons age 18 to 90 years of age. The authors asked which areas of the brain showed the clearest decline in metabolism with age. The strongest association was in the anterior cingulate gyrus. This decline in metabolism in the anterior cingulate may be a reason that aging brings difficulty in self-regulation. However, some studies of aging persons using the conflict score from the ANT found no increase in the time to resolve conflict with age, unless the participants had been diagnosed with Alzheimer's dementia (Fernandez-Duque & Black, 2006).

In another important study, Fair and colleagues (2008) had shown that the functional connectivity as measured by BOLD correlations between the anterior cingulate and more posterior brain areas was very poor in early childhood and showed a marked increase in older ages and adults. A study of resting connectivity in aging adults (Andrews-Hanna, Snyder, Vincent, Lustig, Head, Raichle, & Buckner, 2007) found that the connectivity between midfrontal and posterior areas showed a marked decline in old age. While there was some overlap in strength of connectivity between younger and older adults, the best older adult was only at the mean of the younger adults.

There is also new evidence that meditation methods used with adults to improve executive attention (Tang et al., 2007) can also be used with aged subjects. In this case, the reductions in functional connectivity reported to occur with aging (Andrews-Hanna et al., 2007) can be partly restored following a month of training with Integrative Body-Mind Training (Tang, Lu, Geng, Stein, Yang, & Posner, 2010).

While genotype stays constant over the lifespan, the influence of genes may be even greater in old age than for younger persons. In one study, Nagel and colleagues (2008) reported that the influence of different alleles of the COMT gene on performance on the Wisconsin Card Sorting Task is greater in aged than in younger adults. They accounted for this by arguing that reduced dopamine transmission in the elderly puts them on a part of the U-shaped curve between dopamine transmission and performance that is more sensitive to genetic variation. It is not known if these genetic effects work through the functional connectivity changes discussed in the last paragraph.

Frontal white matter connectivity continues to develop during childhood and adolescence and declines in efficiency in the elderly. Thus, overall, the studies of aging tend to support the general idea that later-developing brain connections may be especially vulnerable to the influence of aging.

## Concluding Remarks

The development of neuroimaging (Posner & Raichle, 1994) and the sequencing of the entire human genome at the end of the twentieth century (Ventner, Adams, Myers, Li, et al., 2001) is making it possible to study the functional anatomy of brain networks, and also to examine how genetic differences might lead to individual variation in the potential to use these networks in the acquisition and performance of skills.

Attention has been an important topic in experimental psychology during the last century and is currently being studied at many levels in cognitive neuroscience. Conceptualizing attention as an organ system with its own functional anatomy and neurophysiology has many beneficial consequences. This approach appears to be very useful for examining many issues related to development.

Understanding maturation processes underlying the development of attentional functions has an interest in itself, but it can also provide the basis for examining cognitive and brain mechanisms involved in attention-related pathologies. In this chapter, we have described data related to the development of the attention networks throughout life. Activation of all three networks is evidenced at different times during the first year of life. Then, further development takes place during childhood. Alerting, which depends on right frontal regions, is increasingly under endogenous control as children become more able to maintain a vigilant state in the absence of external stimulation. Orienting reaches the adult level of maturation by midchildhood. Babies are able to orient attention to external stimulation, showing a progressive increase in the precision of attentional movements. Upon maturation of the superior parietal lobe, children become more efficient in the control of disengagement and voluntary orientation. Finally, the executive attention network shows the longest developmental course of all three networks. Aspects of executive attention appear to be present in infancy; however, the developmental process of this function continues throughout childhood and early adolescence, showing the most significant maturation between 2 and 7 years of age. This network is supported by activation of the anterior cingulate cortex and prefrontal regions, which activation is modulated by dopamine. This network shows a decline in metabolism and functional connectivity at older ages, which could account for the difficulties in self-regulation shown by elderly persons.

The neurocognitive approach also allows examining the interplay between genetic and experience factors that influence the developmental process. Various studies have shown that variations in genes related to neurotransmitters that modulate the activation of the attention networks appear to influence the efficiency of the functioning of these networks in both adults and children. Moreover, polymorphisms of particular attention-related genes (i.e., DRD4 and COMT) appear to interact with environmental factors such as parenting. Some studies have tested polymorphisms in genes that undergo positive selection and therefore are more likely to be transmitted from parents to children. It is of particular interest that the polymorphisms that undergo positive selection appear to be the ones associated with greater environmental influences. This type of data lead to the idea that genetic variation may be selected according to the sensitivity

to environmental influences that they produce in children. This hypothesis needs to be further tested; however, it provides new insights into the old nature/nurture question, supporting the notion of a greater balance between genes and environment.

We have also discussed evidence showing that attention can be improved through training. Data provide support for the idea that training of executive attention during its development moves the underlying network toward more adultlike levels. In addition, the effect of training generalizes to cognitive challenges far removed from the training, such as trials of fluid intelligence and tasks requiring regulation in motivationally relevant situations.

Attention is a crucial element in the development of self-regulation taking place between infancy and later childhood (Rueda, Posner, & Rothbart, 2011). As development proceeds, individual differences in self-regulation are central to such important processes as socialization and the development of schooling skills (Checa, Rodriguez-Bailon, & Rueda, 2008). If attention is considered to be a central system for the successful development of cognitive and emotional regulation of children's behavior, the training of attentional abilities may be an important complement to preschool and early elementary education. Further research is needed to understand to what extent intervention can change attention; however, increased evidence suggests that positive experience (i.e., good parenting, training, appropriate educational methods) may be helpful for optimizing attentional development.

## Questions for Future Research

1. How are attention networks altered during development?

2. What are the mechanisms by which genes influence the organization and efficiency of attention networks?

3. To what extent can training change attention and self-regulation?

4. Do constitutionally based individual differences influence the extent to which attention networks can be modified by experience?

5. Are there limits to the ages at which training can be effective? Do sensitive periods limit attention training?

## Acknowledgments

# References

Ahadi, S. A., Rothbart, M. K., & Ye, R. (1993). Children's temperament in the U.S. and China: Similarities and differences. *European Journal of Personality, 7,* 359–378.

Andrews-Hanna, J. R., Snyder, A. Z., Vincent, J. L., Lustig, C., Head, D., Raichle, M. E., & Buckner, R. L. (2007). Disruption of large-scale brain systems in advanced aging. *Neuron*, 56, 924–935

Auerbach, J. G., Benjamin, J., Faroy, M., Kahana, M., & Levine, J. (2001). The association of the dopamine D4 receptor gene (DRD4) and the serotonin transporter promotor gene (5 HTTL-PR) with temperament in 12-month-old infants. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *42*, 777–783.

Auerbach, J., Geller, V., Letzer, S., Shinwell, E., Levine, J., Belmaker, R. H., & Ebstein, R. P. (1999). Dopamine D4 receptor (D4DR) and serotonin transporter promoter (5-HTTLPR) polymorphisms in the determination of temperament in two month old infants. *Molecular Psychiatry, 4,* 369–374.

Bakermans-Kranenburg, M. J., & van IJzendoorn, M. H. (2006). Gene-environment interaction of the dopamine D4 receptor (DRD4) and observed maternal insensitivity predicting externalizing behavior in preschoolers. *Developmental Psychobiology*, 48, 406–409

Bakersmans-Kranenburg, M. J., Van IJzendoorn, M. H., Pijlman, F. T. A., Mesman, J., & Juffer, F. (2008) Experimental evidence for differential susceptibility: dopamine D4 receptor polymorphism (DRD4 VNTR) moderates intervention effects on toddlers' externalizing behavior in a randomized controlled trial. *Developmental Psychology, 44,* 293–300.

Beauregard, M., Levesque, J., & Bourgouin, P. (2001). Neural correlates of conscious self-regulation of emotion. *Journal of Neuroscience, 21,* RC 165.

Berger, A., Jones, L., Rothbart, M. K., & Posner, M. I. (2000). Computerized games to study the development of attention in childhood. *Behavior Research Methods, Instruments & Computers, 32*(2), 297–303.

Berger, A., Tzur, G., & Posner, M.I. (2006) Infant babies detect arithmetic error. *Proceedings of the National Academy of Sciences USA, 103*, 12649–12553

Blasi, G., Mattay, G. S., Bertolino, A., Elvevåg, B., Callicott, J. H., Das, S., Kolachana, B. S., Egan, M. F., Goldberg, T. E., & Weinberger, D. R. (2005). Effect of catechol-*O*-methyltransferase *val* 158 *met* genotype on attentional control. *Journal of Neuroscience*, *25*(20), 5038–5045.

Block, J. H., & Block, J. (1980). The role of ego-contol and ego-resiliency in the organization of behaviour. In W. A. Collins (Ed.), *Minnesota Symposia on Child Psychology, Vol. 13: Development of cognition, affect, and social relations* (pp. 39–101).

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review, 108,* 624–652.

Broadbent, D. E. (1958). *Perception and communication*. New York: Pergamon.

Bush, G., Luu, P. & Posner, M. I. (2000). Cognitive and emotional influences in the anterior cingulate cortex. *Trends in Cognitive Science, 4/6,* 215–222.

Butcher, P. R. (2000). *Longitudinal studies of visual attention in infants: The early development of disengagement and inhibition of return*. Meppel: Aton.

Canli, T., Omura, K., Haas, B. W., Fallgatter, A., Todd, R., Constable, R. T., & Lesch, K. P. (2005). Beyond affect: A role for genetic variation of the serotonin transporter in neural activation during a cognitive attention task. *Proceedings of the National Academy of Sciences USA, 102*, 12224–12229.

Casey, B., Thomas, K. M., Davidson, M. C., Kunz, K., & Franzen, P. L. (2002). Dissociating striatal and hippocampal function developmentally with a stimulus-response compatibility task. *Journal of Neuroscience, 22*(19), 8647–8652.

Checa, P., Rodriguez-Bailon, R., & Rueda, M. R. (2008). Neurocognitive and temperamental systems of self-regulation and early adolescents' social and academic outcomes. *Mind, Brain and Education, 2*(4), 177–187.

Colombo, J. (2001). The development of visual attention in infancy. *Annual Review of Psychology, 52,* 337–367.

Colombo, J., & Horowitz, F.D. (1987) Behavioral state as a lead variable in neonatal research. *Merrill Palmer Quarterly, 33*, 423–438.

Clohessy, A. B., Posner, M. I., & Rothbart, M. K. (2001). Development of the functional visual field. *Acta Psychologica, 106,* 51–68.

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience, 3*(3), 201–215.

Curtindale, L., Laurie-Rose, C., Bennett-Murphy, L., & Hull, S. (2007). Sensory modality, temperament, and the development of sustained attention: A vigilance study in children and adults. *Developmental Psychology, 43*(3), 576–589.

Danis, A., Pêcheux, M.-G., Lefèvre, C., Bourdais, C., & Serres-Ruel, J. (2008). A continuous performance task in preschool children: Relations between attention and performance. *European Journal of Developmental Psychology, 5*(4), 401–418.

Davidson, M. C., Amso, D., Anderson, L. C., & Diamond, A. (2006). Development of cognitive control and executive functions from 4 to 13 years: Evidence from manipulations of memory, inhibition, and task switching. *Neuropsychologia, 44*(11), 2037–2078.

Davis, E. P., Bruce, J., Snyder, K., & Nelson, C. (2003) The X-trials: Neural correlates of an inhibitory control task in children and adults. *Journal of Cognitive Neuroscience, 13,* 432–443.

Dehaene, S., Posner, M. I., & Tucker, D. M. (1994). Localization of a neural system for error detection and compensation. *Psychological Science, 5,* 303–305.

Diamond, A. (1991). Neuropsychological insights into the meaning of object concept development. In S. Carey & R. Gelman (Eds.), *The epigenesis of mind: Essays on biology and cognition* (pp. 67–110). Hillsdale, NJ: Erlbaum.

Diamond, A., Briand, L., Fossella, J., & Gehlbach, L. (2004). Genetic and neurochemical modulation of prefrontal cognitive functions in children. *American Journal of Psychiatry, 161,* 125–132.

Diamond, A. (2006). The early development of executive functions. In: *Lifespan cognition: Mechanisms of change* (pp. 70–95 xi, 397). New York: Oxford University Press.

Diatchenko, L., Slade, G. D., Nackley, A. G., et al. (2005). Genetic basis for individual variations in pain perception and the development of a chronic pain condition. *Human Molecular Genetics, 14*(1), 135–143.

Ding, Y. C., Chi, H. C., Grady, D. L., Morishima, A., Kidd, J. R., Kidd, K. K., et al. (2002). Evidence of positive selection acting at the human dopamine receptor D4 gene

locus. *Proceedings of the National Academy of Sciences USA, 99*(1), 309–314.

Duncan, J., Seitz, R. J., Kolodny, J., Bor, D., Herzog, H. Ahmed, A., Newell, F. N., & Emslie, H. (2000). A neural basis for general intelligence. *Science, 289,* 457–460.

Durston, S., Thomas, K. M., Yang, Y., Ulug, A. M., Zimmerman, R. D., & Casey, B. (2002). A neural basis for the development of inhibitory control. *Developmental Science, 5*(4), F9–F16.

Enns, J. T., & Brodeur, D. A. (1989). A developmental study of covert orienting to peripheral visual cues. *Journal of Experimental Child Psychology, 48*(2), 171–189.

Enns, J. T., & Cameron, S. (1987). Selective attention in young children: The relations between visual search, filtering, and priming. *Journal of Experimental Child Psychology, 44*, 38–63.

Enns, J. T., & Girgus, J. S. (1985). Developmental changes in selective and integrative visual attention. *Journal of Experimental Child Psychology, 40*, 319–337.

Fair, D., Cohen, A. L., Dosenbach, A. U. F., Church, J. A., Meizin, F. M., Barch, D. M., Raichle, M. E., Petersen, S. E., & Schlagger, B. L. (2008) The maturing architecture of the brain's default network. *Proceedings of the National Academy of Sciences USA, 105*, 4028–4032.

Fair, D. A., Dosenbach, N. U. F., Church, J. A., Cohen, A. L., Brahmbhatt, S., Miezin, F. M., et al. (2007). Development of distinct control networks through segregation and integration. *Proceedings of the National Academy of Sciences USA, 104*(33), 13507–13512.

Fan, J., Fossella, J. A., Summer, T., Wu, Y., & Posner, M. I. (2003) Mapping the genetic variation of executive attention onto brain activity. *Proceedings of the National Academy of Sciences USA, 100,* 7406–7411.

Fan, J., McCandliss, B. D., Sommer, T., Raz, M., & Posner, M. I. (2002). Testing the efficiency and independence of attentional networks. *Journal of Cognitive Neuroscience, 3*(14), 340–347.

Fernandez-Duque, D., & Black, S. E. (2006). Attentional networks in normal aging and Alzheimer's disease. *Neuropsychology, 20*, 133–143.

Fossella, J., Posner, M. I., Fan, J., Swanson, J. M., & Pfaff, D. M. (2002). Attentional phenotypes for the analysis of higher mental function. *Scientific World Journal, 2,* 217–223.

Fox, N. A., Hane, A. A., & Pine, D. S. (2007). Plasticity for affective neurocircuitry—How the environment affects gene expression. *Current Directions in Psychological Science, 16*(1), 1–5.

Fox, N. A., Nichols, K. E., Henderson, H. A., Rubin, K. H., Schmidt, L. A., Hamer, D., et al. (2005). Evidence for a gene–environment interaction in predicting behavioral inhibition in middle school children. *Psychological Science, 16*(12), 921–926.

Friedman, N. P., Miyake, A., Young, S. E., DeFries, J. C., Corley, R. P., & Hewitt, J. K. (2008). Individual differences in executive functions are almost entirely genetic in origin. *Journal of Experimental Psychology: General, 137*, 201–225.

Garon, N., Bryson, S. E., & Smith, I. M. (2008) Executive function in preschoolers: A review using an integrative framework. *Psychological Bulletin, 134,* 31–60.

Gehring, W. J., Gross, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science, 4*, 385–390.

Gerardi-Caulton, G. (2000). Sensitivity to spatial conflict and the development of self-regulation in children 24–36 months of age. *Developmental Science, 3*(4), 397–404.

Gray, J. A., & McNaughton, N. (1996). *The neuropsychology of anxiety: Reprise.* Paper presented at the annual meeting of the Nebraska Symposium on Motivation: Perspectives on anxiety, panic and fear. Volume 43, Lincoln, NB.

Green, C. S., & Bavelier, D. (2003). Action video game modifies visual selective attention. *Nature, 423*(6939), 534–537.

Green, C. S., & Bavelier, D. (2006). Effect of action video games on the spatial distribution of visuospatial attention. *Journal of Experimental Psychology: Human Perception and Performance, 32*(6), 1465–1478.

Haith, M. M., Hazan, C., & Goodman, G. S. (1988). Expectation and anticipation of dynamic visual events by 3.5 month old babies. *Child Development, 59,* 467–469.

Harman, C., Rothbart, M. K., & Posner, M.I. (1997). Distress and attention interactions in early infancy. *Motivation and Emotion, 21,* 27–43.

Harpending, H., & Cochran, G. (2002). In our genes. *Proceedings of the National Academy of Sciences USA, 99,* 10–12.

Hillyard, S. A., Di Russo, F., & Martinez, A. (2006) The imaging of visual attention. In J. Duncan & N. Knwisher (Eds.), *Attention and performance XX: Functional brain imaging of visual cognition* (Chapter 19, pp. 381–388). Oxford, UK: Oxford University Press.

Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: reinforcement learning, dopamine and error-related negativity. *Psychological Review, 109*, 679–709.

James, W. (1890). *The Principles of Psychology.* New York, H. Holt and Company.

Johnson, M. H., & Morton, J. (1991). *Biology and cognitive development: The case of face recognition.* Oxford: Blackwell.

Johnson, M. H., Posner, M. I., & Rothbart, M. K. (1991). Components of visual orienting in early infancy: Contingency learning, anticipatory looking and disengaging. *Journal of Cognitive Neuroscience, 3*(4), 335–344.

Johnstone, S. J., Pleffer, C. B., Barry, R. J., Clarke, A. R., & Smith, J. L. (2005). Development of inhibitory processing during the Go/NoGo task: A behavioral and event-related potential study of children and adults. *Journal of Psychophysiology, 19*(1), 11–23.

Jones, L. B., Rothbart, M. K., & Posner, M. I. (2003). Development of executive attention in preschool children. *Developmental Science, 6*(5), 498–504.

Jonkman, L. M., Lansbergen, M., & Stauder, J. E. A. (2003). Developmental differences in behavioral and event-related brain responses associated with response preparation and inhibition in a go/no go task. *Psychophysiology, 40*(5), 752–761.

Jonkman, L., Sniedt, F., & Kemner, C. (2007). Source localization of the Nogo-N2: A developmental study. *Clinical Neurophysiology, 118*(5), 1069–1077.

Jonkman, L. M. (2006). The development of preparation, conflict monitoring and inhibition from early childhood to young adulthood; A Go/No go ERP study. *Brain Research, 1097*(1), 181–193.

Kagan, J. (1998). Biology and the child. In N. Eisenberg (Ed.), *Handbook of child psychology: Vol. 3. Social, emotional, and personality development* (5th ed., pp. 177–235). New York: Wiley.

Kahneman, D. (1973). *Attention and effort.* Englewood Cliffs, NJ: Prentice Hall.

Kaufman, A. S., & Kaufman, N. L. (1990). *Kaufman Brief Intelligence Test—Manual.* American Guidance Service, Circle Pines.

Keele, S. W., Ivry, R. B., Mayr, U., Hazeltine, E., & Heuer, H. (2003). The cognitive and neural architecture of sequence representation. *Psychological Review, 110*, 316–339.

Kerns, K. A., Eso, K., & Thomson, J. (1999). Investigation of a direct intervention for improving attention in young children with ADHD. *Developmental Neuropsychology, 16*(2), 273–295.

Kerr, A., & Zelazo, P.D. (2004). Development of "hot" executive function: The Children's Gambling Task. *Brain and Cognition, 55,* 148–157.

Klingberg, T., Forssberg, H., & Westerberg, H. (2002). Training of working memory in children with ADHD. *Journal of Clinical and Experimental Neuropsychology, 24*(6), 781–791.

Kochanska, G. (1995). Children's temperament, mothers' discipline, and security of attachment: Multiple pathways to emerging internalization. *Child Development, 66,* 597–615.

Kochanska, G., Murray, K., & Coy, K. C. (1997). Inhibitory control as a contributor to conscience in childhood: From toddler to early school age. *Child Development, 68,* 263–277.

Koop, B., Rist, F., & Mattler, U. (1996). N200 in the flanker task as a neurobehavioral tool for investigating executive control. *Psychophysiology, 33,* 282–294.

Kremen, A. M., & Block, J. (1998). The roots of ego-control in young adulthood: Links with parenting in early childhood. *Journal of Personality and Social Psychology, 75,* 1062–1075.

Lamm, C., Zelazo, P. D., & Lewis, M. D. (2006). Neural correlates of cognitive control in childhood and adolescence: Disentangling the contributions of age and executive function. *Neuropsychologia, 44*(11), 2139–2148.

Levy, F. (1980). The development of sustained attention (vigilance) in children: Some normative data. *Journal of Child Psychology and Psychiatry, 21*(1), 77–84.

Lin, C. C. H., Hsiao, C. K., & Chen, W. J. (1999). Development of sustained attention assessed using the Continuous Performance Test among children 6–15 years of age. *Journal of Abnormal Child Psychology, 27*(5), 403–412.

Mackworth, J. F. (1969). *Vigilance and habituation.* London: Pergamon.

Marrocco, R. T., & Davidson, M. C. (1998). Neurochemistry of attention. In R. Parasuraman (Ed.), *The attentive brain* (pp. 35–50). Cambridge, MA: MIT Press.

Meltzoff, A. N., & Moore, M. K. (1977). Imitation of facial and manual gestures by human neonates. *Science, 198,* 74–78.

Meyer, D. E., & Kieras, D. E. (1997) A computational theory of executive cognitive processes and multiple task performance: Part 1. Basic mechanisms. *Psychological Review, 104,* 3–65.

Mezzacappa, E. (2004). Alerting, orienting, and executive attention: Developmental properties and sociodemographic correlates in an epidemiological sample of young, urban children. *Child Development, 75*(5), 1373–1386.

Morrison, F. J. (1982). The development of alertness. *Journal of Experimental Child Psychology, 34*(2), 187–199.

Nagel, I. E., Chicherio, C., Li, S. C., von Oertzen, T., Sander, T., Villringer, A., Heekeren, H. R., Backman, L., & Lindenberger, U. (2008). Human aging magnifies genetic effects on executive functioning and working memory. *Frontiers in Human Neuroscience.*

NICHD Early Child Care Research Network. (1993). *The NICHD Study of Early Child Care: A comprehensive longitudinal study of young children's lives.* ERIC Document Reproduction Service No. ED3530870.

Norman, D. A., & Shallice, T. (1986) Attention to action: willed and automatic control of behavior. In R. J. Davison, G. E. Schwartz, & D. Shapiro (Eds.), *Consciousness and self-regulation* (pp. 1–18). New York: Plenum Press.

Ochsner, K. N., Bunge, S. A., Gross, J. J., & Gabrieli, J. D. E. (2002). Rethinking feelings: An fMRI study of the cognitive regulation of emotion. *Journal of Cognitive Neuroscience, 14,* 1215–1229.

Olesen, P. J., Westerberg, H., & Klingberg, T. (2004). Increased prefrontal and parietal activity after training of working memory. *Nature Neuroscience, 7*(1), 75–79.

Pardo, J. V., Lee, J. T., Sheikh, S. A., Surerus-Johnson, C., Shah, H., Munch, K. R., Carlis, J. V., Lewis, S. M., Kuskowski, M. A., & Dysken, M. W. (2007). Where the brain grows old: Decline in anterior cingulate and medial prefrontal function with normal aging. *NeuroImage, 35,* 1231–1237.

Parasuraman, R., Greenwood, P.M., Kumar, R., & Fossella, J. (2005). Beyond heritability: Neurotransmitter genes differentially modulate visuospatial attention and working memory. *Psychological Science, 16*(3), 200–207.

Pelphrey, K. A., Reznick, J. S., Goldman, B. D., Sasson, N., Morrow, J., Donahoe, A., & Hodgson, K. (2004). Development of visuospatial short-term memory in the second half of the first year. *Developmental Psychology, 40*(5), 836–851.

Posner, M. I. (1978). *Chronometric explorations of mind.* Hillsdale, NJ: Lawrence Erlbaum Associates.

Posner, M. I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology, 32*(1), 3–25.

Posner, M. I., & Petersen, S. E. (1990). The attention system of human brain. *Annual Review of Neuroscience, 13,* 25–42.

Posner, M. I., & Raichle, M. E. (1994). *Images of mind.* New York: Scientific American Library: Dist. W.H. Freeman.

Posner, M. I., & DiGirolamo, G. J. (1998). Executive attention: Conflict, target detection, and cognitive control. In R. Parasuraman (Ed.), *The attentive brain* (pp. 401–423). Cambridge, MA: MIT Press.

Posner, M. I. (2008). Measuring alertness. *Annals of the New York Academy of Sciences, 1129* (Molecular and Biophysical Mechanisms of Arousal, Alertness, and Attention), 193–199.

Posner, M. I., & Fan, J. (2008). Attention as an organ system. In J. R. Pomerantz (Ed.), *Topics in integrative neuroscience* (Chapter 2, pp. 31–61). New York: Cambridge University Press.

Posner, M. I., & Rothbart, M. K. (2007). Research on attention networks as a model for the integration of psychological science. *Annual Review of Psychology, 58,* 1–23.

Posner, M. I., Rothbart, M. K., & Sheese, B. E. (2007). Attention genes. *Developmental Science, 10,* 24–29.

Posner, M. I., Rueda, M. R., & Kanske, P. (2007). Probing the mechanisms of attention. In J. T. Cacioppo, J. G. Tassinary, & G. G. Berntson (Eds.), *Handbook of psychophysiology* (3rd ed., pp. 410–432). Cambridge, UK: Cambridge University Press.

Prencipe, A., & Zelazo, P. D. (2005). Development of affective decision-making for self and other: Evidence for the integration of first- and third-person perspectives. *Psychological Science, 16,* 501–505.

Raz, A., & Buhle, J. (2006). Typologies of attentional networks. *Nature Reviews Neuroscience, 7,* 367–379.

Reuter, M., Ott, U., Vaidl, D., & Henning, J. (2007). Impaired executive attention is associated with a variation in the promotor region of the tryptophan hydroxylase-2 gene. *Journal of Cognitive Neuroscience, 19,* 401–408.

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Richards, J. E., & Hunter, S. K. (1998). Attention and eye movements in young infants: neural control and development. In J. E. Richards (Ed.), *Cognitive neuroscience of attention* (pp. 131–162). Mahwah, NJ: Erlbaum.

Ridderinkhof, K. R., & van der Molen, M. W. (1995). A psychophysiological analysis of developmental differences in the ability to resist interference. *Child Development, 66*(4), 1040–1056.

Rothbart, M. K. (1988). Temperament and the development of inhibited approach. *Child Development, 59*, 1241–1250.

Rothbart, M. K., Ahadi, S. A., & Hershey, K. L. (1994). Temperament and social behavior in childhood. *Merrill-Palmer Quarterly, 40,* 21–39.

Rothbart, M. K., Ahadi, S. A., Hershey, K. L., & Fisher, P. (2001). Investigations of temperament at three to seven years: The Children's Behavior Questionnaire. *Child Development, 72*, 1394–1408.

Rothbart, M. K., & Bates, J. E. (2006). Temperament in children's development. In W. Damon & R. Lerner (book eds.) & N. Eisenberg (vol. ed.), *Handbook of child psychology: Vol. 3, Social, emotional, and personality development* (6th ed., pp. 99–166). New York: Wiley.

Rothbart, M. K., Ellis, L. K., Rueda, M. R., & Posner, M. I. (2003). Developing mechanisms of effortful control. *Journal of Personality, 71,* 1113–1143.

Rothbart, M. K., & Posner, M. I. (2006). Temperament, attention, and developmental psychopathology. In *Developmental psychopathology, Vol. 2: Developmental neuroscience* (2nd ed., pp. 465–501). Hoboken, NJ: John Wiley & Sons Inc.

Rothbart, M. K., & Rueda, M. R. (2005). The development of effortful control. In U. Mayr, E. Awh, & S. W. Keele (Eds.), *Developing individuality in the human brain: A Festschrift honoring Michael I. Posner* (pp. 167–188). Washington, DC: American Psychological Association..

Rueda, M., Posner, M. I., & Rothbart, M. K. (2005). The development of executive attention: Contributions to the emergence of self-regulation. *Developmental Neuropsychology, 28*(2), 573–594.

Rueda, M., Fan, J., McCandliss, B. D., Halparin, J. D., Gruber, D. B., Lercari, L. P., et al. (2004a). Development of attentional networks in childhood. *Neuropsychologia, 42*(8), 1029–1040.

Rueda, M. R., Checa, P., & Cómbita, L. M. (2012). Enhanced efficiency of the executive attention network after training in preschool children: Immediate changes and effects after two months. *Developmental Cognitive Neuroscience, 2S,* S192–S204.

Rueda, M. R., Posner, M. I., & Rothbart, M. K. (2011). Attentional control and self-regulation. In K. D. Vohs & R. F. Baumeister (Eds.), *Handbook of self-regulation: Research, theory and applications* (2nd ed., pp. 284–299). New York: The Guilford Press.

Rueda, M. R., Posner, M. I., Rothbart, M. K., & Davis-Stober, C. P. (2004b). Development of the time course for processing conflict: An event-related potentials study with 4-year-olds and adults. *BMC Neuroscience, 5*(39), 1–13.

Rueda, M. R., Rothbart, M. K., McCandliss, B. D., Saccomanno, L., & Posner, M. I. (2005). Training, maturation, and genetic influences on the development of executive attention. *Proceedings of the National Academy of Sciences USA, 102*(41), 14931–14936.

Rueda, M. R., Rothbart, M. K., Saccomanno, L., & Posner, M. I. (2007). Modifying brain networks underlying self-regulation.

In *Adolescent psychopathology and the developing brain: Integrating brain and prevention science* (pp. 401–419). New York: Oxford University Press.

Santesso, D. L., Segalowitz, S. J., & Schmidt, L. A. (2005). ERP correlates of error monitoring in 10-year olds are related to socialization. *Biological Psychology, 70,* 79–87.

Salthouse, T. A. (2005). Relations between cognitive abilities and measures of executive functioning. *Neuropsychology, 19*, 532–545.

Schaffer, H. R. (1974) Cognitive components of infants' response to strangeness. In M. Lewis & L. A. Rosenbloom (Eds.), *The origins of fear* (pp. 11–24). New York: Wiley.

Schul, R., Townsend, J., & Stiles, J. (2003). The development of attentional orienting during the school-age years. *Developmental Science, 6*(3), 262–272.

Segalowitz, S. J., & Davies, P. L. (2004). Charting the maturation of the frontal lobe: An electrophysiological strategy. *Brain and Cognition, 55*(1), 116–133.

Segalowitz, S. J., Unsal, A., & Dywan, J. (1992). Cleverness and wisdom in 12-year-olds: Electrophysiological evidence for late maturation of the frontal lobe. *Developmental Neuropsychology, 8,* 279–298.

Sheese, B. E., Rothbart, M. K., Posner, M. I., White, L., & Fraundorf, S. (2008). Executive attention and self-regulation in infancy. *Infant Behavior & Development, 31*(3), 501–510.

Sheese, B. E., Voelker, P., Posner, M. I., & Rothbart, M. K. (2009). Genetic variation influences on the early development of reactive emotions and their regulation by attention. *Cognitive Neuropsychiatry, 14*(4), 332–355.

Sheese, B. E., Voelker, P. M., Rothbart, M. K., & Posner, M. I. (2007). Parenting quality interacts with genetic variation in dopamine receptor DRD4 to influence temperament in early childhood. *Development & Psychopathology, 19,* 1039–1046.

Sohlberg, M. M., McLaughlin, K. A., Pavese, A., Heidrich, A., & Posner, M. I. (2000). Evaluation of attention process training and brain injury education in persons with acquired brain injury. *Journal of Clinical and Experimental Neuropsychology, 22*(5), 656–676.

Swanson, J., Oosterlaan, J., Murias, M., Schuck, S., Flodman, P., Spence, M. A., Wasdell, M., Ding, Y., Chi, H., Smith, M., Mann, M., Carlson, C., Kennedy, M. J., Sergeant, J., Leung, P., Zhang, Y., Sadeh, A., Chen, C., Moyzis, R., & Posner, M. I. (2000). Attention deficit/hyperactivity disorder children with a 7-repeat allele of the dopamine receptor D4 gene have extreme behavior but normal performance on critical neuropsychological tests of attention. *Proceedings of National Academy of Sciences USA, 97,* 4754–4759.

Tang, Y. Y., Lu, Q., Geng, X., Stein, E. A., Yang, Y., & Posner, M. I. (2010). Short-term meditation induces white matter changes in the anterior cingulate. *Proceedings of the National Academy of Sciences of the USA, 107*(35), 15649–15652.

Tang, Y., Ma, Y., Wang, J., Fan, Y., Feng, S., Lu, Q., Yu, Q, Sui, D., Rothbart, M. K., Fan, J., & Posner, M. I. (2007). Short-term meditation training improves attention and self-regulation. *Proceedings of the Nationall Academy of Sciences USA, 104,* 17152–17156.

Tucker, D. M., Hartry-Speiser, A., McDougal, L., Luu, P., & deGrandpre, D. (1999). Mood and spatial memory: emotion and right hemisphere contribution to spatial cognition. *Biological Psychology, 50,* 103–125.

Veen, V., & Carter, C. S. (2002). The timing of action-monitoring processes in the anterior cingulate cortex. *Journal of Cognitive Neuroscience, 14*, 593–602.

Ventner, J. C., Adams, M. D., Myers, E. W., Li, P. W., Mural, R. J., et al. (2001). The sequence of the human genome. *Science, 291,* 1304–1335.

Voelker, P., Sheese, B. E., Rothbart, M. K., & Posner, M. I. (2009). Variations in Catechol-O-Methyltransferase Gene interact with parenting to influence attention in early development. *Neuroscience, 164*(1), 121–130.

Wainwright, A., & Bryson, S. E. (2002). The development of exogenous orienting: Mechanisms of control. *Journal of Experimental Child Psychology, 82*(2), 141–155.

Wainwright, A., & Bryson, S. E. (2005). The development of endogenous orienting: Control over the scope of attention and lateral asymmetries. *Developmental Neuropsychology, 27*(2), 237–255.

Walter, G. (1964). The convergence and interaction of visual, auditory and tactile responses in human non-specific cortex. *Annals of the New York Academy of Sciences, 112,* 320–361.

Wang, E. T., Kodama, G., Baldi, P., & Moyzis, R. K. (2006). Global landscape of recent inferred Darwinan selection for *Homo sapiens. Proceedings of the National Academy of Science USA, 103*, 135–140.

Wynn, K. (1992). Addition and subtraction by human infants. *Nature, 358,* 749–750.