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JAMES ARTHUR LECTURE ON
THE EVOLUTION OF THE HUMAN BRAIN
MARCH 2007

EVOLUTION AND DEVELOPMENT
OF SELF-REGULATION

MICHAEL I. POSNER

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EVOLUTION AND DEVELOPMENT OF SELF-REGULATION*

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*Published versions of these lectures can be obtained from Publications, Dept. of Anthropology, The American Museum of Natural History, Central Park West at 79th St., New York, N.Y. 10024.

**Out of print.

†Published version: *The Brain in Hominid Evolution*, New York: Columbia University Press, 1971.

James Anthony

JAMES ARTHUR

1842–1930

Born in Ireland and brought up in Glasgow, Scotland, James Arthur came to New York in 1871. Trained in mechanics and gear-cutting, he pursued a career in the manufacture and repair of machinery, during the course of which he founded a number of successful businesses and received patents on a variety of mechanical devices. His mechanical interests evolved early into a lifelong passion for horology, the science of measuring time, and he both made some remarkable clocks and assembled an important collection of old and rare timepieces.

Early in this century James Arthur became associated with the American Museum of Natural History, and began to expand his interest in time to evolutionary time, and his interest in mechanisms to that most precise and delicate mechanism of them all, the human brain. The ultimate expression of his fascination with evolution and the brain was James Arthur's bequest to the American Museum permitting the establishment of the James Arthur Lectures on the Evolution of the Human Brain. The first James Arthur Lecture was delivered on March 15, 1932, two years after Mr. Arthur's death, and the series has since continued annually, without interruption.

EVOLUTION AND DEVELOPMENT OF SELF-REGULATION

I was very pleased to receive the invitation to deliver the 77th James Arthur Lecture on the Evolution of the Human Brain. Although the work done in our laboratory has more to do with development (Posner and Rothbart, 2007) than with evolution, Geary (2005) has provided a strong perspective on how mental processes, including control mechanisms, arise in evolution, and I am very glad to be able to place our studies of self-regulation within this more general evolutionary context. Fortunately for this effort, all parents are well aware of the remarkable transformation from infancy to childhood as their children develop the ability to regulate emotions and to persist with goals in the face of distractions.

The achievements of this period are usually labeled “self-regulation.” Self-regulation is defined by one researcher as “the key mediator between genetic predisposition, early experience and adult functioning” (Fonagy and Target, 2002). Although self-regulation has been seen as primarily an issue in child development, its genetic basis suggests an important evolutionary history. In fact, a number of genes have been identified as related to the brain network that we believe underlies self-regulation (Posner et al., 2007). Our approach has been to understand the anatomy of self-regulation through the use of neuroimaging and then to examine how genes and experience develop this network within individuals. This allows us to discuss evolutionary changes in the network that take place specifically between nonhuman primates and humans, as well as more recent changes that might reflect aspects of human evolution. This lecture will concern both aspects of evolution.

ANATOMY

A frontal executive attention network (see fig. 1) that includes the anterior cingulate and lateral prefrontal cortex is active in different tasks that involve attention when conflict is present and/or producing a nonhabitual response is required (Botvinick et al., 2001). One important study (Duncan et al., 2000) examined a wide range of

Fig. 1. Triangles mark the anatomy of the network involved in self-regulation from imaging studies. The anatomy for alerting and orienting is also shown (from Posner and Rothbart, 2007).

verbal, spatial, and object tasks selected from intelligence tests that had in common a strong loading on the factor of general intelligence. These items were contrasted with perceptually similar control items that did not require the kind of attention and thought involved in general intelligence. This subtraction led to differential activity in two major areas. One was the anterior cingulate and the second was lateral prefrontal cortex.

Conflict

Many imaging studies have been conducted using either the Stroop task or variants of it that involve conflict among elements (Bush et al., 2000). The Stroop task requires that a person respond to the color of ink in which a competing color word is represented (fig. 2a). In the version of the Stroop task that was used with primates trained to appreciate the quantity of a digit (see fig. 2b) it was found that both humans and macaques took additional time to re-

spond during conflict trials. In fact the increase in reaction time (RT) was about the same for the two species, but while humans rarely made an error even after many hundreds of training trials, macaques made errors at the rate of almost 25% on the conflict trials, suggesting that their network for resolving conflict is not as efficient (Washburn, 1994). We examined three conflict tasks, two of which were suitable for children, using the same adults and MRI scanner to determine areas of activation (Fan et al., 2003). We found that all three tasks had a common focus in the anterior cingulate and, in addition, all activated similar areas of the lateral prefrontal cortex.

The more dorsal area of the anterior cingulate has been shown to be active primarily in cognitive tasks like the Stroop. However, when tasks have a more emotional component they activate a more ventral part of the cingulate (Bush et al., 2000). We have argued that these two areas are involved in regulation of cognitive and emotional networks (see fig. 3).

Connectivity

A possible difference between humans and other primates is in their control of cognition and emotion, and may lie in the close connectivity that the cingulate has to other parts of the brain. As illustrated in figure 3, the dorsal part of the anterior cingulate is involved in the regulation of cognitive tasks, while the more ventral part of the cingulate is involved in regulation of emotion. One way to examine this issue is to image the structural connections of different parts of the cingulate using diffusion tensor imaging. This form of imaging uses the diffusion of water molecules in particular directions due to the presence of myelinated fibers. Thus it provides a way of examining the physical connections present in the brains of people. Diffusion tensor imaging was carried out while people performed a conflict-related task, and it was found that the dorsal part of the anterior cingulate cortex (ACC) was connected to cortical areas of the parietal and frontal lobes, while the ventral part of the ACC had strong connections to subcortical limbic areas (Posner et al., 2006).

Comparative anatomical studies point to important differences in

Fig. 2. (a) Stroop color-of-ink test in which a competing color word is represented. (b) An adaptation of the Stroop task used by Washburn (1994) with trained monkeys and humans. The task is to move a mouse to the larger of the two arrays. When the size of the array conflicts with the quantity of digits, humans (and monkeys trained to appreciate numbers) show an increase in RT and errors.

the evolution of cingulate connectivity between nonhuman primates and people. Anatomical studies show the great expansion of white matter, which has increased more in recent evolution than has the neo cortex itself (Zilles, 2005). One type of projection cell called

Fig. 3. A division of the anterior cingulate into a dorsal area related to regulation of cognitive networks and a ventral division related to regulation of emotional networks (adapted from Bush et al., 2000).

Fig. 4. Diagram showing control of cognitive networks from the dorsal anterior cingulate (adapted from Posner and Raichle, 1996).

the Von Economo neuron is found only in the anterior cingulate and a related area of the anterior insula (Allman et al., 2005). It is thought that this neuron is important in communication between the cingulate and other brain areas. This neuron is not present at all in macaques and expands greatly in frequency between great apes and humans. The two brain areas in which von Economo neurons are found (cingulate and anterior insula) are also shown to be in close communication even during the resting state (Dosenbach et al., 2007). Moreover, there is some evidence that the frequency of this type of neuron also increases during development between infancy and later childhood (Allman et al., 2005). In our view (1) these neurons, and the rapid and efficient connectivity they provide, are a major reason why self-regulation in adult humans can be so much stronger than in other organisms, and (2) the development of this system may relate to the achievements in self-regulation that we have documented between infancy and age 7–8 (see fig. 11). This form of regulation is illustrated in the diagram in figure 4 that shows the close connection between the dorsal anterior cingulate and areas of the brain related to perception, language, and action. Because of the regulation provided by the brain network involving the cingulate, we call this the *executive attention network*.

It is possible to use fMRI to examine the functional connectivity

between brain areas during the performance of a task (Posner et al., 2006). Two recent studies illustrate the use of fMRI to trace the interaction of the anterior cingulate with other brain areas. In one study subjects were required to switch between auditory and visual modalities (Crottaz-Herbette and Mennon, 2006). The dorsal anterior cingulate was coupled either to visual or auditory sensory areas depending on the selected modality. Another study (Etkin et al., 2006) required subjects to resolve conflict related to negative emotion. The ventral anterior cingulate was shown to be coupled to the amygdala in this form of conflict resolution. Studies requiring people to control their positive (Beauregard et al., 2001) or negative emotional reaction (Ochsner et al., 2001) to stimuli have shown strong activation in the anterior cingulate compared to studies where subjects viewed the stimuli without the instruction for self-regulation.

INDIVIDUALITY

The finding that common brain networks are involved in self-regulation provides one important approach to human evolution by looking at commonalities and differences with nonhuman organisms. However, another approach of equal importance involves an examination of differences in the efficiency of this network among individuals. Such differences could rest in part upon genetic variation known to exist among individuals and in part upon differences in cultural or individual experience between people. The study of temperament examines individual differences in reactivity and self-regulation that are biologically based (Rothbart and Bates, 2006).

Effortful Control

One of the most important of the individual differences has been called "effortful control." It is a higher-order factor consisting of a number of subscales. In children it involves subscales of attention, focus shifting, and inhibitory control. For example, caregivers answer questions such as: "when playing alone, how often is your child distracted, how often does your child look immediately when you point?" or adults may be asked "how often do you make plans you do not follow through?" The answers are aggregated for various

scales. Factor analysis produces common factors, which, like effortful control, summarize several of the scales.

Effortful control has been linked to brain areas involved in self-regulation by imaging studies (Whittle, 2007). Whittle had 155 adolescents fill out a temperament scale (Ellis and Rothbart, 2001) and also measured the size of different brain structures and their activity. The results of her study are shown in figure 5. She found that the dorsal anterior cingulate size was positively correlated to effortful control and that the ventral anterior cingulate activity was negatively related to effortful control. The reciprocal relation between the ventral and dorsal cingulate has also been reported in other imaging studies (Drevets and Raichle, 1998).

Attention Network Test

In our work we have used the Attention Network Test (ANT) to examine the efficiency of brain networks that underlie three functions of attention: alerting, orienting and executive attention (Fan et al., 2002). The task examined by ANT, illustrated in figure 6, requires that the person press one key if the central arrow points to the left and another if it points to the right. Conflict is introduced by having surrounding flankers either point in the same (congruent) or opposite (incongruent) condition. Cues presented prior to the target provide information on either where or when the target will occur. The reaction times for the separate conditions shown in figure 6 are subtracted (see bottom of fig. 6) to provide three numbers that represent the skill of each individual in alerting, orienting and executive networks. In a sample of 40 normal persons (Fan et al., 2002) we found each of these numbers to be reliable over repeated presentations. In addition, we found no correlation among the numbers. An analysis of the reaction times for this task shows significant effects for cue type and for the type of target. There were only two small interactions that indicated some lack of independence among the cue conditions. One of these interactions was that orienting to the correct target location tended to reduce the influence of the surrounding flankers. In addition, omitting a cue, which produces relatively long reaction times, also reduces the size of the flanker in-

Fig. 5. The dorsal and ventral anterior cingulate have been found to correlate with the effortful control measure by the Early Adolescent Behavior Questionnaire (Ellis and Rothbart, 2001). [Figure adapted from Whittle, 2007]

terference. Presumably this is because some of the conflict is reduced during the time the subject is preparing to process the target location.

A subsequent study using fMRI (Fan et al., 2005) showed that the brain areas that are involved for these three networks, as shown in figure 1 are for the most part independent. Figure 7 names the brain areas that represent the source of the alerting, orienting, and executive (conflict) attention networks. Each of the networks has a dominant neuromodulator arising from subcortical brain areas.

The scores on the executive attention (conflict) network of the ANT have been shown to correlate with the temperament factor called “effortful control” (EC) at several ages during childhood. Gerardi-Caulton (2000) carried out some of the first research linking

EC to underlying brain networks of executive attention, using a spatial conflict as a laboratory marker task. Similar findings linking parent-reported temperament EC to performance on laboratory attention tasks have been described for 24-, 30-, and 36-month-olds (Rothbart et al., 2003), 3- and 5-year-olds (Chang and Burns, 2005), and for 7-year-olds (Gonzales et al., 2001).

Daily Life

Effortful control and the ANT executive attention scores have been related to many aspects of child development. Effortful control is related to the empathy that children show toward others, the ability to delay an action, and the ability to avoid such behaviors as lying or cheating when given the opportunity in laboratory studies (Rothbart and Rueda, 2005). There is also evidence that high levels of effortful control and enhanced ability to resolve conflict are related to fewer antisocial behaviors such as truancy in adolescents (Ellis et al., 2004).

Genotypes

We genotyped 200 normal New York adults who were tested with the ANT. We examined several candidate genes including the Dopamine 4 Receptor Gene, which had previously been related to both the Attention Deficit Hyperactivity Disorder and to a personality trait called sensation seeking (Auerbach et al., 2001; Swanson et al., 1998). We found that alleles of this gene were related to performance on the conflict subtraction of the ANT, but that these alleles did not produce significant differences in RT, or on the other subtractions. In addition, we found that a different polymorphism of this gene was related to the strength of activation in the anterior cingulate during a brain scan conducted while the persons performed the ANT (Fan et al., 2005).

However, there was a great puzzle in these data. The allele related to ADHD and sensation seeking was the 7 repeat, but it was the presence of the 4 repeat that produced the most difficulty in resolving conflict. In addition, Swanson and his associates (Swanson et al., 2000) found that the 7 repeat, while more likely to be present

Fig. 6. A schematic of the attention network test. (a) Various cues that inform people about the location and time of the target, (b) congruent and incongruent target conditions, (c) time line for the cue and target, and (d) three subtractions that indicate the quantitative efficiency of each network.

in children with ADHD, was not associated with attentional difficulties. Moyzis and associates showed that the 7 repeat was one of some 300 genes influencing neural function (Wang et al., 2006) that gave evidence of being positively selected in recent human evolution (Ding et al., 2002). These findings suggested that the association of the 7 repeat with ADHD might have been via its relationship with sensation seeking, rather than through poor attention. We believe that the data provided below from our current longitudinal study (see fig. 10) might help resolve this paradox and suggest why it is that some genetic alleles like the 7 repeat may increase their frequency in human evolution.

Posner et al. (2007) have recently summarized evidence for several dopamine and serotonin-related genes that have specific relationships to the executive attention network. It is now clear that part of the difference among individuals on ANT scores is related to

these genetic variations. In the next section we will consider how experiences of the infant and child relate to these genetic variations in shaping the executive network.

DEVELOPMENT

We (Posner and Rothbart, 2007) have been interested in how the attention system develops in infancy and early childhood. The development of executive attention can be easily observed both by questionnaire and cognitive tasks after about age 3–4, when parents can identify the ability of their children to regulate their emotions and control their behavior in accord with social demands. However, in infancy it has been difficult to pose questions that refer to effortful control because most regulation seems automatic or involves the caregiver's intervention. Obviously infants cannot be instructed to press a key in accord with a particular rule.

Longitudinal Study

We have been examining executive attention in infancy with a view to seeing if we can predict later executive attention and effortful control from infant behavior. One study examined the ability of infants of 7 months to detect errors (Berger et al., 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 was active in adults was 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. The results, as illustrated in figure 8, indicated that the same EEG component over the same electrode sites differed between conditions in infants and adults. Since this EEG component had been shown to come from the anterior cingulate gyrus (Dehaene et al., 1994) it appears that the same

FUNCTION	STRUCTURES	MODULATOR
Orient	Superior parietal	<u>Acetylcholine</u>
	Temporal parietal junction	
	Frontal eye fields	
	Superior colliculus	
Alert	Locus Coeruleus	Norepinephrine
	Right frontal and parietal cortex	
Executive attention	Anterior cingulate	Dopamine
	Lateral ventral prefrontal	
	Basal ganglia	

Fig. 7. The three attention networks and the anatomical structures that are the source of their influence and the neurochemical modulator shown to be dominant for each network.

Fig. 8. When seeing errors, 7-month-old infants show an increase in negativity in comparison with seeing the correct answer (a). This difference is similar although it occurs a bit later than that found in adults (b) and comes from the anterior cingulate (Berger et al., 2006).

brain anatomy is involved as in adult studies. Of course, the result of activating this anatomy for observing an error is not the same as the activation in adults for self-made errors, where the adults 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.

We also began a longitudinal study with infants of 7 months (Sheese et al., in prep.). We studied eye movements that occurred when attractive stimuli appeared in fixed sequence of locations on a screen in front of the child. On most occasions the children moved their eyes to the stimulus, but on some occasions they moved their eyes to the location at which the stimulus would occur prior to it being presented. We argued that the anticipatory movements were an early form of voluntary response because they actually anticipated the visual event (see fig. 9). To introduce conflict we used the sequence 1-2-1-3, where given a stimulus at 1 the infant would not know to move to 2 or 3 without a consideration of what had happened before. In support of the idea that the anticipatory movements reflected the executive attention system, we found that 3.5-year-olds showed a correlation between performance in voluntary key-press tasks and the tendency to make correct anticipations in the visual sequence study (Rothbart et al., 2003).

In the first session of our longitudinal study we used two other tasks, the first in which the infants were presented with novel objects and the second in which they saw somewhat disturbing masks (Sheese et al., in prep.). Anticipatory looking was related to more hesitant initial approach to the toys, including longer latencies to initial reaching, and longer duration of looking without physically touching the toy. Infants rated by their parents as higher in Positive Affect (often called Surgency) showed lower latencies to physically engage the toys, and higher frequencies of engagement. These results suggest that an early form of executive attention may allow for the modulation of positive affect and related approach tendencies. Anticipatory looking was also positively related to greater use of sucking as a self-soothing mechanism during the mask presentation. These results indicate that anticipatory looking is related both to caution in reaching toward novel toys, and to aspects of the reg-

Visual Sequence Task

Fig. 9. An apparatus for studying attention in infants. The infants' eyes are recorded on camera 1 and camera 2 shows the stimuli. Shifts of the head and eyes to the various locations are taped and the times and directions measured. The stimuli are a fixed sequence of locations such as: upper left, lower, upper left, upper right 1-2-1-3 (after Rothbart et al., 2003).

ulation of distress in infancy. They also suggest that executive attention is present in infancy and serves as one basis for the regulation of emotion.

Genes and Parenting

We have had the children tested at 7 months brought back at 18–21 months. This time we added an additional task 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). Although all of the parents were likely concerned and caring, they did differ in their scores, and we divided them at the mean into two groups. One of the groups had a higher quality of parenting, and the other a lower quality. We also geno-

typed the children for several candidate genes including the DRD4 gene that had been related to ADHD and sensation seeking (see above).

One finding with the DRD4 gene (Sheese et al., 2007) seems to have important implications beyond the study of one particular molecule. We found, as shown in figure 10, that in the presence of the 7-repeat allele, there was a strong influence of parental quality. Parents who were rated as giving greater support, autonomy etc., had children that were average in a reported aggregate we called sensation seeking, consisting of activity level, impulsivity, and risk taking. Children given somewhat lower-quality parenting, however, showed extremely high levels of sensation seeking. For children without the 7 repeat, parental quality did not have a significant influence. Our sensation-seeking aggregate comes from caregiver reports on their child's temperament, but its constituents are similar to symptoms frequently reported by children with ADHD. Thus we think that the paradox of the 7 repeat may arise because its presence can produce symptoms of ADHD without attention deficits, but its presence does not automatically lead to later problems; that depends upon environmental influences such as parenting. Similar evidence that environment can have a stronger influence in the presence of the 7 repeat has been reported by others (Bakermans-Kranenburg and van Ijzendoorn, 2006; van Ijzendoorn and Bakermans-Kranenburg, 2006).

Positive selection of the 7-repeat allele could well arise from the sensitivity to environmental influences that it may help to make possible. Parenting allows the culture to train children in the values that it favors. For example, Rothbart and colleagues (Ahadi et al., 1993) found that in Western culture effortful control appears to regulate negative affect (sadness and anger), while in China (at least in the 1980s) it was found to regulate positive affect (outgoingness and enthusiasm). In recent years the nature/nurture interaction has tilted very much to the importance of genes, but if genetic variations are selected according to their influence on the sensitivity of the child to cultural influences, this could support a balance between genes and environment. Theories of positive selection in the DRD4 gene have stressed the role of sensation seeking in human evolution (Har-

(a)

(b)

(c)

pending and Cochran, 2002; Wang et al., 2004). Our new findings do not contradict this emphasis but may provide one explanation that could have even wider significance. It remains to be seen whether the other 300 genes estimated to show positive selection would also relate to environmental factors. We will be examining additional longitudinal data to test these ideas further.

Later Childhood

Gerardi-Caulton (2000) carried out some of the first research linking effortful control (EC) to underlying brain networks of executive attention. Executive attention is typically measured in conflict situations such as the Stroop task. Because children of preschool age do not typically read, location and identity rather than word meaning and ink color served as the dimensions in the spatial conflict task. Children sat in front of two response keys, one located to the child's left and one to the right. Each key displayed a picture, and on every trial, a picture identical to one of the pair appeared on either the left or right side of the screen. Children were rewarded for responding to the identity of the stimulus, regardless of its spatial compatibility with the matching response key (Gerardi-Caulton, 2000).

Reduced accuracy and slowed reaction times for spatially incompatible trials relative to spatially compatible trials reflected the effort required to resolve conflict between identity and location. Performance on this task produced a clear interference effect in adults and activated the anterior cingulate (Fan et al., 2003). Children 24 months of age tended to use one response regardless of what was correct, while 36-month-old children performed at high accuracy levels but, like adults, responded more slowly and with reduced accuracy to conflict trials. At 3 years of age and older, the time to resolve conflict was negatively

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Fig. 10. Three child temperament scales: (a) Activity level, (b) high-intensity pleasure (risk taking) and (c) impulsivity showing an interaction between parenting in presence or absence of the 7-repeat allele of the DRD4 gene (after Sheese et al., submitted). In the presence of the 7 repeat, parenting quality matters much more to child temperament.

Age	Overall Performance		Conflict Scores	
	Overall R T (ms)	Overall accuracy (% errors)	RT (ms)	Accuracy (% errors)
4.5	1599	12.79	207	5.8
6	931	15.8	115	15.6
7	833	5.7	63	0.7
8	806	4.9	71	-0.3
9	734	2.7	67	1.6
10	640	2.2	69	2.1
adults	483	1.2	61	1.6

Fig. 11. Reaction time and accuracy in the ANT overall performance and in the conflict-related executive network scores as a function of age. The 4.5-year-olds come from a separate study (after Rueda et al., 2004).

correlated with parent reports of temperamental EC and positively related to the child's rated negative affect.

The development of executive attention has also been traced into the primary school period (Rueda et al., 2004) using a child version of the ANT. The results of several studies using the ANT are shown in figure 11. In this version of the ANT, children judge in which direction a fish is swimming, and fish flankers that surround the target indicate either the same (congruent) or opposite (incongruent) response. Cues prior to the target allow the measurement of all three attentional networks: orienting, alerting, and executive attention, as described in figure 6d. Reaction times for the children were much longer than for adults, but they showed similar independence among the three networks. Rather surprisingly, the ability to resolve conflict on the flanker task, as measured by the ANT, remained about the same from age 7 to adulthood.

There is considerable evidence that the executive attention network is important in many aspects of behavior, including the acquisition of school subjects such as literacy, and in a wide variety of other subjects that draw upon general intelligence. Anatomically the network involving resolution of conflict also overlaps with brain areas related to general intelligence (Duncan et al., 2000). Training of attention, either explicitly or implicitly, is also often a part of the school curriculum (Posner and Rothbart, 2007), but additional stud-

ies are needed to determine exactly how and when attention training can best be accomplished and its long lasting importance.

Training Exercises

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 gene $\times$ environment interaction (see fig. 10) 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 et al., 2000) as well as in children with ADHD (Kerns et al., 1999). Work with ADHD children has also shown that working-memory training can improve attention (Klingberg et al., 2002; Olesen et al., 2004). With normal adults, training with video games produced better performance on a range of visual attention tasks (Green and Bavelier, 2003).

To examine the role of experience on the executive attention network, we developed and tested a 5-day training intervention that uses computerized exercises. We tested the effect of training during the period of major development of executive attention, which takes place between 4 and 7 years of age (Rueda et al., 2005). We hoped to develop methods that could be used to observe improvements in conflict resolution following training. EEG data (see fig. 12) showed clear evidence of improvement in network efficiency in resolving conflict following training. The N2 component of the scalp recorded averaged electrical potential has been shown to arise in the anterior cingulate and is related to the resolution of conflict (van Veen and Carter, 2002). We found N2 differences between congruent and incongruent trials of the ANT in trained 6-year-olds that resembled differences found in adults. In the 4-year-olds, training seemed to influence more anterior electrodes that have been related to emotional control areas of the cingulate (Bush et al., 2000). These data

ERP time courses of the conflict resolution

Fig. 12. (b) Event-related potentials recorded during the ANT from adults, trained six-year-old, and untrained six-year-old control subjects. The dark tracing is from the conflict trials and the light tracing from congruent trials. The trained children show a greater negativity after about 400 milliseconds on incongruent trials, similar to what was found for adults, but untrained children did not show this effect. The electrodes showing the effect in (b) have been localized to the anterior cingulate (after Rueda et al., 2005).

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 intelligence in the trained group compared to the control children. This finding suggested that training effects had generalized to a measure of cognitive processing that is far removed from the training exercises. We did not observe changes in temperament over the course of the training, but this was expected due to the short time elapsing between assessment sessions. We hope our training method will be evaluated along with other such methods both as possible means of improving attention prior to school and for children diagnosed with ADHD and

other attention-related disorders (see, for example, Tamm et al., in press). However, we don't have any expectation that our exercises are optimal or even better than other methods.

The study of attention training as a whole suggests that networks can be shaped both in informal ways and by formal training. With the availability of imaging methods it should be possible to design appropriate methods for children of various ages and with various forms of difficulty. Our studies certainly support the importance of educational designs in improving the lives of children.

SUMMARY

Human beings can regulate their thoughts, emotions, and actions: for example, by passing up an immediate reward for a larger delayed reward. Progress in neuroimaging and in sequencing the human genome make it possible to think about self-regulation in terms of a specific neural network that includes midline and lateral frontal areas.

A number of cognitive tasks involving conflict as well as efforts to exercise control of emotions have been shown to activate similar frontal brain areas. Studies have traced the development of this network from about 2.5 to 7 years of age. At this age range, children can carry out instructed tasks and parents can describe their ability to regulate behavior in a variety of situations. We have recently begun to examine the earlier forms of self-regulation in infants of 7 months. These studies suggest that executive attention can be studied by anticipatory eye movements to repeating locations. Other studies show that infants, like adults, can detect errors. Detection of errors by infants appears to involve an anatomy similar to that present in adults. Individual differences in the development of the executive attention network have been related to parental reports of the ability of children to regulate their behavior, to delay reward, and to develop a conscience. In adolescents these individual differences predict the propensity for antisocial behavior.

Differences in specific dopamine genes are related to individual efficiency in performance, and to the degree of activation of this network in imaging studies. Humans, to a greater degree than other

primates, are able to plan ahead, resist distraction, and maintain a goal orientation. These human characteristics appear to depend upon the efficiency of self-regulation. Many of the brain areas involved are shared with other animals, providing a perspective on how self-regulation has evolved. Animal studies may make it possible to learn in detail how genes influence the common brain network underlying self-regulation.

A number of neurological and psychiatric pathologies involve difficulties in self-regulation and show deficits in the underlying attentional network. Specific training experiences have been shown to influence the development of this network in children. Imaging may help us understand how network improvement relates to treatment of some mental disorders.

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