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The Attention System of the Human Brain: 20 Years After

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Abstract

Here, we update our 1990 *Annual Review of Neuroscience* article, “The Attention System of the Human Brain.” The framework presented in the original article has helped to integrate behavioral, systems, cellular, and molecular approaches to common problems in attention research. Our framework has been both elaborated and expanded in subsequent years. Research on orienting and executive functions has supported the addition of new networks of brain regions. Developmental studies have shown important changes in control systems between infancy and childhood. In some cases, evidence has supported the role of specific genetic variations, often in conjunction with experience, that account for some of the individual differences in the efficiency of attentional networks. The findings have led to increased understanding of aspects of pathology and to some new interventions.

Keywords

alerting network; executive network; orienting network; cingulo-opercular network; frontoparietal network

INTRODUCTION

Twenty years ago, when neuroimaging was in its infancy, we summarized the current state of knowledge on attention in the 1990 volume of the *Annual Review of Neuroscience* (Posner & Petersen 1990). At that time, most available evidence was from behavioral studies of normal adults or patients with varying forms of brain injury. However, the ability to image brain activity with positron emission tomography seemed to hold great promise for the physiological analysis of mental processes, including attention. In our review, we were able to integrate findings of the initial imaging studies. We never imagined that the growth of cognitive neuroscience over the subsequent 20 years would make it possible to revisit our analysis, with 4,000–6,000 imaging papers on attention or cognitive control and nearly 3,500 citations of our original review.

The original review suggested three basic concepts about the attention system. The first is that the attention system is anatomically separate from processing systems, which handle incoming stimuli, make decisions, and produce outputs. We emphasized the sources of the attentional influences, not the many processing systems that could be affected by attention. The second concept is that attention utilizes a network of anatomical areas. The third is that

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these anatomical areas carry out different functions that can be specified in cognitive terms. The most unique aspect of our original article, which separated it from the many excellent summaries of the attention literature appearing in the *Annual Review of Neuroscience* in the years since, is the discrete anatomical basis of the attention system: divided into three networks, each representing a different set of attentional processes. We believe that these important concepts are still operative. Here, we try to update the framework of our earlier *Annual Review* article [other summaries are available in Posner (2012a,b)].

In this review, we outline some of the major advances related to our framework that have taken place in the past 20 years. First, we reintroduce the three original networks of the attention system. We examine the nature of these networks and how the ideas related to them have evolved. The second part of the article explores additions to the original conception. Two new networks are proposed with their functional descriptions, and new methods for understanding interactions between them. The third part of the article indicates how the ideas have been extended to related topics, for example, in tying genetic variations to individual differences in network efficiency and in examining the development of attention in childhood.

THE ORIGINAL NETWORKS

The three networks we described in 1990 included an alerting network, which focused on brain stem arousal systems along with right hemisphere systems related to sustained vigilance; an orienting network focused on, among other regions, parietal cortex; and an executive network, which included midline frontal/anterior cingulate cortex. Each of these networks is explored below.

Alerting

The concept of arousal goes back to the classic work of Moruzzi & Magoun (1949) on the role of the brain stem reticular system in maintaining alertness (Figure 1, for macaque brain). As more became known of the neuromodulatory systems of the brain stem and thalamus, it was necessary to qualify the general concept of arousal into more differentiated components. Within cognitive psychology, a major emphasis has been on producing and maintaining optimal vigilance and performance during tasks; this is the sense of alertness that we discussed in our 1990 article.

One approach to the study of alerting is to use a warning signal prior to a target event to produce a phasic change in alertness. The warning cue leads to replacing the resting state with a new state that involves preparation for detecting and responding to an expected signal. If a speeded response is required to the target, reaction time improves following a warning. This improvement is not due to the buildup of more accurate information about the target, which is not changed by the warning signal, but the warning signal does change the speed of orienting attention and thus responding to the signal.

Several other methods have been used to study tonic alertness. These include changes over the course of the day (circadian rhythm). Reaction times are usually longer in the early morning and decline over the course of the day only to rise again during the night and peak in the early morning (Posner 1975). These measures reflect other diurnal changes such as body temperature and cortisol secretion. A long established approach to tonic alertness is to use a long and usually rather boring task to measure sustained vigilance. Some of these tasks have grown out of the job of radar operators looking for near-threshold changes over long periods of time. Vigilance tasks rely heavily on mechanisms of the right cerebral cortex (Posner & Petersen 1990). Both classical lesion data and more recent imaging data confirm that tonic alertness is heavily lateralized to the right hemisphere.

Orienting

The orienting network is focused on the ability to prioritize sensory input by selecting a modality or location. Although the arguments in the original review included discussion of the pulvinar and the superior colliculus, most of our focus was on visual selection and on the parietal cortex as part of a posterior attention system (Figure 2*a*). Consensus in the imaging literature now indicates that frontal as well as posterior areas are involved in orienting. For example, human and animal studies have implicated the frontal eye fields (FEF) in this process (Corbetta et al. 1998, Thompson et al. 2005).

In addition, parietal areas have been implicated in related forms of processing. This processing can be concrete as in the specification of directed motor or eye movements (Lindner et al. 2010) or more abstract as “movements” across a number line (Hubbard et al. 2005). In fact, the specificity of parietal regions in terms of sensory versus motor processing is a major point of contention. Nonetheless, most would agree the functions of the parietal lobe are not restricted to orienting to sensory stimuli but involve other related processes.

Executive

In our original article, the third major system was presented under the heading of target detection. The main reason for this was not that target detection itself is a major attentional process, but that the moment of target detection captures awareness in a very specific way. Although it is possible to monitor for targets in many processing streams without too much difficulty, the moment of target detection produces interference across the system, slowing detection of another target (Duncan 1980). This set of processes is related to the limited capacity of the attention system, and to awareness itself, and has often been called focal attention. One might think of focal attention as the entry to the conscious state, which may involve widespread connections from the midline cortex and the anterior cingulate cortex (ACC) (Figure 2*b*) to produce the global work space frequently associated with consciousness (Dehaene & Changeux 2011). We associated target detection and awareness of the target with the medial frontal cortex and the adjacent ACC. This brain region has been highly studied by imaging experiments partly because of its frequent activation.

Although one of us (S.P.) has vacillated significantly on this original idea over the past 20 years, it seems that the idea is still relevant. One of the reasons is that the ACC and related regions have been reliably activated when there is conflict [e.g., a requirement to withhold a dominant response to perform a subdominant response (Botvinick et al. 2001)]. The argument has been extended to include a role for these areas in the regulation of both cognition and emotion (Bush et al. 2000).

The most compelling argument for a focal attention explanation comes from the activity found in the medial frontal/anterior cingulate in such diverse operations as perception of either physical (Rainville et al. 1997) or social (Eisenberger et al. 2003) pain, processing of reward (Hampton & O’Doherty 2007), monitoring or resolution of conflict (Botvinick et al. 2001), error detection (Dehaene et al. 1994), and theory of mind (Kampe et al. 2003). These different demands all activate this region, in most cases in conjunction with the anterior insula. Some investigators advocate a separate role for the system for each of the comparisons above (e.g., as part of a pain or reward system), but, as we argue below, we support a more comprehensive view that captures more of the results, including focal attention and the regulation of processing networks. Since the original article, this network has also taken on an even more extensive role in executive control on the basis of findings showing multiple top-down control signals in these regions. This more complex functional and anatomical network is discussed in the executive control section below.

ELABORATIONS OF THE FRAMEWORK

The intervening 20 years since our original article have produced a surprising amount of support for the basic outlines of the framework described above. There has also been a significant amount of elaboration or evolution of the ideas during that timeframe. The next three sections review some of the studies deepening or expanding our understanding of the original networks.

Alerting

Our understanding of the physiology and pharmacology underlying the alerting system has changed significantly. For example, strong evidence relates the neuromodulator norepinephrine (NE) to the alerting system. A warning signal is accompanied by activity in the locus coeruleus, the source of NE (Aston-Jones & Cohen 2005). Warning-signal effects can be blocked by drugs such as guanfacine and clonodine, which decrease NE release (Marrocco & Davidson 1998). Drugs that increase NE release can also enhance the warning-signal effect. The NE pathway includes major nodes in the frontal cortex and in parietal areas relating to the dorsal but not the ventral visual pathways (Morrison & Foote 1986).

To examine the specificity of these effects to the warning signal, researchers used a cued detection task with humans, monkeys, and rats (Beane & Marrocco 2004, Marrocco & Davidson 1998) to separate information about where a target will occur (orienting) from when it will occur (alerting). To accomplish this, one of four cue conditions was presented prior to a target for a rapid response. By subtracting a double cue condition, where the participant is informed of when a target will occur but not where, from a no cue condition, they receive a specific measure of the warning influence of the signal. When the cue that indicates the target’s location is subtracted from an alerting cue, the difference represents effects of orienting. Results of drug studies with humans and monkeys show that NE release influences alerting effects, whereas drugs influencing the neuromodulator acetylcholine (Ach) affect orienting but not alerting. Studies have shown that individual differences in alerting and orienting are largely uncorrelated (Fan et al. 2002) and that orienting improves to the same degree with a cue regardless of the level of alertness. These results suggest a great deal of independence between these two functions (Fernandez-Duque & Posner 1997). However, these systems usually work together in most real-world situations, when a single event often provides information on both when and where a target will occur (Fan et al. 2009).

The changes during the time between warning and target reflect a suppression of ongoing activity thought to prepare the system for a rapid response. In the central nervous system there is a negative shift in scalp-recorded EEG, known as the contingent negative variation (CNV) (Walter 1964), which often begins with the warning signal and may remain present until the target presentation. This negative potential appears to arise in part from the anterior cingulate and adjacent structures (Nagai et al. 2004) and may overlap the event-related response to the warning stimulus. The negative shift may remain present as a standing wave over the parietal area of the contralateral hemisphere (Harter & Guido 1980). If the target interval is predictable, the person may not show the CNV until just prior to target presentation.

An extensive imaging study (Sturm & Willmes 2001) showed that a largely common right hemisphere and thalamic set of areas are involved in both phasic and tonic alerting. Another imaging study, however, suggested that the warning signal effects rely more strongly on left cerebral hemisphere mechanisms (Coull et al. 2000, Fan et al. 2005). This could represent the common findings described above on hemispheric differences in which right lateralized processes often involve slower effects (tonic), whereas left hemisphere mechanisms are more likely to be involved with higher temporal (phasic) or spatial frequencies (Ivry & Robertson 1997). The exact reasons for differences in laterality found with tonic and phasic studies are still unknown.

Orienting

In a series of imaging experiments using cuing methodology in combination with event-related fMRI, Corbetta & Shulman (2002) showed that two brain systems are related to orienting to external stimuli as illustrated in Figure 2*a*. A more dorsal system including the FEFs and the interparietal sulcus followed presentation of an arrow cue and was identified with rapid strategic control over attention. When the target was miscued, subjects had to break their focus of attention on the cued location and switch to the target location. The switch appeared to involve the temporoparietal junction (TPJ) and the ventral frontal cortex and was identified with the interrupt signal that allowed the switch to occur.

The dorsal system included the well-studied parietal regions but added a small set of frontal locations as well, particularly in the FEFs. Some have argued that covert attention shifts are slaved to the saccadic eye movement system (Rizzolatti et al. 1987), and neuroimaging studies using fMRI have shown that covert and overt shifts of attention involve similar areas (Corbetta et al. 1998). However, single-unit physiology studies in the macaque suggest important distinctions at the level of cell populations, with some cells in the FEFs active during saccades and a distinct but overlapping population of cells involved in covert shifts of attention (Schafer & Moore 2007, Thompson et al. 2005). The cells responsible for covert shifts of attention also seem to hold the location of cues during a delay interval (Armstrong et al. 2009). The two populations of cells are mixed within the FEFs and, at least to date, have not been distinguished by fMRI. However, the physiological data indicate that covert attention is distinct from the motor system governing saccades, even though they clearly interact.

As suggested by the FEF studies, it is important to be able to link the imaging and physiological results with other studies to provide more details on local computations. One strategy for doing so is to study the pharmacology of each of the attention networks. Cholinergic systems arising in the basal forebrain appear to play a critical role in orienting; lesions of the basal forebrain in monkeys interfere with orienting attention (Voytko et al. 1994). However, it appears that the site of this effect is not in the basal forebrain per se, but instead involves the superior parietal lobe. Davidson & Marrocco (2000) made injections of scopolamine directly into the lateral intraparietal area of monkeys. This area corresponds to the human superior parietal lobe and contains cells influenced by cues about spatial location. The injections have a large effect on the monkey’s ability to shift attention to a target. Systemic injections of scopolamine, an anticholinergic, have a smaller effect on covert orienting of attention than do local injections in the parietal area. Cholinergic drugs do not affect the ability of a warning signal to improve the monkey’s performance, so there appears to be a double dissociation, with NE involved mainly in the alerting network and Ach involved in the orienting network. These observations in the monkey have been confirmed by similar studies in the rat (Everitt & Robbins 1997). It is especially significant that comparisons in the rat studies of cholinergic and dopaminergic mechanisms have shown that only the former influence the orienting response (Everitt & Robbins 1997, Stewart et al. 2001).

The more ventral network including the TPJ (Figure 2*a*) seemed to be more active following the target and was thus identified as part of a network responsive to sensory events. It is strongly right lateralized and lesions in this area are central to the neglect syndrome, although the interaction of TPJ with more frontal and dorsal brain areas is also critical (Shulman & Corbetta 2012). Researchers generally agree about the membership of the major nodes of the orienting network on the basis of both spatial cuing and visual search studies (Hillyard et al. 2004, Wright & Ward 2008).

Perhaps more surprising is that the brain areas involved in orienting to visual stimuli seem to overlap strongly (within fMRI resolution) with those involved with orienting to stimuli in other modalities (Driver et al. 2004). Although attention operates on sensory-specific modalities according to the incoming target, the sources of this effect appear to be common. There are also important synergies between modalities. In many cases, orienting to a location will provide priority not only to the expected modality but also to information present at the same location from other modalities (Driver et al. 2004), indicating how closely the sensory systems are integrated within the orienting network.

How can the sources of the orienting network described above influence sensory computations? Anatomically, the source of the orienting effect lies in the network of parietal, frontal, and subcortical areas mentioned above. However, the influence of attention is on the bottom-up signals arriving in sensory-specific areas: for vision, in the primary visual cortex and extrastriate areas moving forward toward the temporal lobe. That this remote influence involves synchronization between activity in the more dorsal attention areas and activity in the more ventral visual areas is an influential idea (Womelsdorf et al. 2007). The synchronization apparently leads to greater sensitivity in the visual system, allowing faster responses to visual targets and thus improved priority for processing targets.

In addition to synchronization, single-unit physiology studies conducted within ventral visual areas suggest that as items are added to a visual scene they tend to reduce the firing rate of cells responding to the target stimulus. Attention to a target seems to reduce the influence of other competing stimuli. This idea was important in the development of biased competition theory (Desimone & Duncan 1995). This theory sees attention as arising out of a winner-take-all competition within various levels of sensory and association systems. fMRI studies confirm that attention to a stimulus can occur prior to its arrival, changing the baseline neural and blood oxygen level–dependent (BOLD) response, and that the overall BOLD activity is affected in ways consistent with the biased competition theory (Desimone & Duncan 1995).

Executive Control

Our third original network has been elaborated considerably. As noted above, our original focus was on midline regions of the medial frontal cortex and anterior cingulate. We suggested that activity found during the performance of tasks was related to focal attention because trial-related activity in these regions was greater for targets than for nontargets, for conflict more than for nonconflict trials, and for errors more than for correct trials. We argued that such a system might be very useful for producing top-down regulation, thus its relationship to executive control. This role of the ACC in top-down control was based on rather slim evidence at the time but seems to still seems to be accurate and plays an important role in two prominent theories of executive control in the current literature. One theory stresses the role of the ACC in monitoring conflict and in relation to lateral frontal areas in resolving the conflict (Botvinick et al. 2001, Carter & Krug 2012). A different view arguing for two different top-down control networks is based on extensive studies of the specific aspects of the ACC during task performance and correlations with other regions at rest (Figure 2*b*,*c*) (Dosenbach et al. 2006, 2007).

Support for two separate executive control networks arises from studies designed to discover signals related to top-down task control. Such signals might include those related to task instructions that are transient at the beginning of a task block (Figure 3). Transient block transition signals had been seen in earlier work (Donaldson et al. 2001, Fox et al. 2005, Konishi et al. 2001) with many different interpretations. A second type of activity is sustained across the trials of the task, putatively related to the maintenance of task parameters/top-down control (Figure 3). The third type of signal is related to performance feedback; an example of such feedback would be systematic differences between correct and incorrect trials (Figure 3).

Dosenbach et al. (2006) studied 10 different tasks (including visual and auditory words and visual objects as stimuli, with many different decision criteria, such as semantic, timing, and similarity judgments) searching for evidence of these signal types. Lateral frontal and parietal regions appeared to emphasize transient signals at the beginning of blocks, whereas medial frontal/cingulate cortex and bilateral anterior insula also showed sustained maintenance signals across task conditions. Although these experiments identified a set of regions that could be involved in top-down task level control, they provide no evidence of the relationships between regions.

Another experiment (Dosenbach et al. 2007) looked for functional correlations (at rest) between regions that showed some or all of these putative control signals, with the idea that these “functional connections” may define the systems-level relationships between the regions. Lateral frontal and parietal regions that showed primarily start-cue activity correlated well with each other (Figure 2*c*). The midline and anterior insular regions that showed additional sustained activity also correlated well with each other (Figure 2*c*), but these two sets of regions did not correlate strongly with each other.

These results suggested there are two separable executive control networks. Detailed evidence for this view is found in Dosenbach et al. (2008). The frontoparietal network appears to be distinct from the orienting network discussed previously, whereas the cingulo-opercular network overlaps with the original executive network. If this view is correct, there are two relatively separate executive networks. Although the best imaging evidence shows that the orienting and frontoparietal executive networks are separate in adulthood, they may have a common origin in early development (see Self-Regulation section, below).

This breakdown of executive control into two separate networks is anatomically similar to an influential idea pertaining to cognitive control (Botvinick et al. 2001, Carter & Krug 2012). However, this cognitive control view favors a single unified executive system in which lateral prefrontal cortex provides top-down control signals, guided by performance-monitoring signals generated by midline structures. Although the cognitive control view and the ideas shown in Figure 2 are anatomically similar, several specific functional differences remain. In the dual network view (Dosenbach et al. 2008), the two executive systems act relatively independently in producing top-down control. The cingulo-opercular control system shows maintenance across trials and acts as stable background maintenance for task performance as a whole. The frontoparietal system, in contrast, showing mostly start-cue signals, is thought to relate to task switching and initiation and to adjustments within trials in real time. Both the cognitive control view and the dual networks view explain a considerable amount of extant data, but we believe there are several reasons to choose the latter formulation.

First, lesion studies in both humans and animals seem to indicate separate aspects of control. Large lesions of the frontal midline often result in akinetic mutism in which people are capable of carrying out goal-directed activities but do not do so. On the other hand, patients with more laterally placed lesions, including those in the dorsolateral prefronal cortex (DLPFC) often exhibit perseverations with an inability to switch from one set to the other. In a compelling set of macaque experiments, Rossi et al. (2007) showed that a complete unilateral resection of the DLPFC and an interruption of the corpus callosum resulted in a unilateral inability to switch sets but an intact ability to adopt a sustained set, consistent with the human lesion data.

A second difference between the dual network and cognitive control views is concerned with the directionality of relationships. The cognitive control view requires a timing difference between the midline monitoring processes and the DLPFC implementation regions within a trial. The two-network account is tolerant of ordering effects because the two networks operate separately. Two quite different sets of data argue that cingulo-opercular involvement is often at the end of or after the trial. The first is from studies of single-unit activity in the ACC in macaques (Ito et al. 2003). During a saccade countermanding task, investigators found neurons that signaled errors and unexpected rewards after trial completion. Second, a recent human imaging study by Ploran et al. (2007) used a slow reveal task. During visual information processing, activity progressively increased with increasing visual information across several seconds in the DLPFC. This preceded late activity in the ACC and anterior insula. These results are consistent with the hypothesis that the ACC may often serve to monitor the consequences of actions, and they are inconsistent with a more rigid directionality.

The addition of two separate orienting networks and two separate executive networks raises the possibility that additional control networks will be elaborated in the future. However, for several reasons, we do not expect the number of control networks to be much larger than the number described here. The study of many complex systems, from ecosystems to protein-protein interactions, seems to indicate that these systems follow a “rule of hand” and have approximately five controlling variables (ranging from three to seven) (Gunderson & Holling 2002). For example, the maintenance of upright balanced posture appears to be controlled by at least three separate systems: vision, the vestibular system, and kinesthetic joint sensors. These systems act relatively independently and have different spatial and temporal characteristics. From this perspective, the presence of five relatively separate attention networks appears reasonable. A second argument in favor of this view is an empirical one. In a recent large-scale study of resting state networks (Power et al. 2011), with effectively all the brain represented, all the cortical networks, found by the more piecemeal approaches described above, are present.

EXTENDING THE FRAMEWORK

One of the gratifying outcomes of our original publication has been the many ways that these ideas inspired a large number of studies. We review extensions of the framework into new areas related to attention networks.

Self-Regulation

The ability to control our thoughts, feelings, and behavior in developmental psychology is called self-regulation; with adults it is often called self-control (see sidebar on Will, Self-Regulation, and Self-Control for further definitions). Neuroimaging presents strong evidence that conflict tasks such as the Stroop effect activate common areas of the anterior cingulate gyrus: the dorsal portion for more strictly cognitive tasks and the ventral area for emotion-related tasks (Botvinick et al. 2001, Bush et al. 2000). Although the cingulate anatomy is much more complex, the division into cognitive and emotion-related areas has been supported by more detailed anatomical studies (Beckmann et al. 2009).

WILL, SELF-REGULATION, AND SELF-CONTROL

Several names have been applied to the voluntary control of emotion and cognition. During child development, these functions are often called self-regulation. This name provides a clear contrast to the regulation that occurs through the caregiver or other external sources. In adults, the same set of voluntary functions is frequently called self-control. Regulation may also occur through nonvoluntary means, for example, by fear or by the calming aspects of drugs or therapy. In all cases, self-control or self-regulation appears to be an ability to control reflexive or otherwise dominant responses to select less dominant ones.

Conflict tasks

The Stroop effect involves the conflict between the task of naming the color of ink of conflicting color names (e.g., the word GREEN presented in RED INK). The Stroop and other conflict-related tasks have been used to measure the ability to select the less dominant response. Because the classic Stroop effect requires reading, other conflict tasks such as spatial conflict, flanker conflict, and pictorial conflict have also been used. Imaging studies with adults suggest that the conflict in these tasks have a common anatomy (Fan et al. 2003a).

Anatomy

The use of imaging has provided some evidence of a common brain network that is involved in all these senses of control. This network includes anterior cingulate (Bush et al. 2000) and anterior insula (Dosenbach et al. 2007; Sridharan et al. 2007, 2008) and also includes areas of the prefrontal cortex when inhibition of dominant responses is a strong feature (Fan et al. 2003a). The common involvement of the anterior cingulate in attention and both emotion and cognitive control has provided one basis for the argument that the executive attention network is critical to these various functions. The brain activation of conflict-related tasks such as the Stroop has also been common to studies of attention and aspects of control.

Age

Self-regulation has been a concept used mainly in developmental psychology, whereas the terms cognitive control, self-control, and willpower are usually applied to adults. There appears to be no strict dividing line. A new finding is the important role of the orienting system in providing some of the control in infants and in young children (Posner et al. 2012, Rothbart et al. 2011). Even in adults, no doubt orienting to new sensory stimuli or thoughts can be a self-control mechanism.

Future

The much broader term executive function is applied in psychology to self-control as well as the ability to solve problems, shift tasks, plan ahead, and implement goals. Although conflict resolution has been studied widely with normals, the anatomy of other functions remains to be thoroughly explored.

Support for the voluntary exercise of self-regulation comes from studies that examine either the instruction to control affect or the connections involved in the exercise of that control. For example, the instruction to avoid arousal during processing of erotic events (Beauregard et al. 2001) or to ward off emotion when looking at negative pictures (Ochsner et al. 2002) produces a locus of activation in midfrontal and cingulate areas. If people are required to select an input modality, the cingulate shows functional connectivity to the selected sensory system (Crottaz-Herbette & Menon 2006) and in emotional tasks to limbic areas (Etkin et al. 2006).

Both behavioral and resting state functional data suggest substantial development of the executive attention network between infancy and childhood. A study of error detection in seven-month-old infants and adults (Berger et al. 2006) shows that both ages use the anterior cingulate area, but the usual slowing following an error does not seem present until about three years of age (Jones et al. 2003). We recently proposed (Posner et al. 2012, Rothbart et al. 2011) that during infancy control systems depend primarily on the orienting network as described previously. During later childhood and into adulthood, the time to resolve conflict correlated with parent reports of their child's ability to control his or her behavior (effortful control, EC) (Posner & Rothbart 2007, Rothbart et al. 2011). The correlation between conflict scores and parent reports of EC form one basis for the association between self-regulation and executive attention. EC is also related to the empathy that children show toward others and their ability to delay an action as well as to avoid such behaviors as lying or cheating when given the opportunity. High levels of EC and the ability to resolve conflict are related to fewer antisocial behaviors in adolescents (Rothbart 2011). These findings show that self-regulation is a psychological function crucial for child socialization, and they suggest that it can also be studied in terms of specific anatomical areas and their connections by examining the development of executive attention networks.

Differences in Network Efficiency

Although everyone has the attention networks described above, there are also individual differences in the efficiency of all brain networks. The Attention Network Test (ANT) has been used to examine the efficiency of attention networks (Fan et al. 2002). The task requires the person to press one key if the central arrow points to the left and another if it points to the right. Conflict is introduced by having flankers surrounding the target pointing in either the same (congruent) or opposite (incongruent) direction as the target. Cues presented prior to the target provide information on where or when the target will occur. There are strong individual differences in each attention network and there are surprisingly low correlations between these network scores (Fan et al. 2002), although the networks interact in more complex tasks and in everyday life (Fan et al. 2009).

Normal functions including attention are undoubtedly influenced by many genes in complex interaction with epigenetic and environmental factors. Most studies have involved various pathologies and have not centered on common human functions; hence relatively little is known about the full range of genes involved in attention networks. One strategy would be to use emerging genomic and epigenomic technologies to carry out studies of large cohorts using various attention tasks as phenotypes to determine genes that relate to performance differences. A more limited approach, based on what is known about attention networks, takes advantage of the association between different neuromodulators and attention networks to examine specific genetic alleles (e.g., related to dopamine) to examine individual performance on the appropriate network (see Green et al. 2008 for review). As one example, the ANT has been used to examine individual differences in the efficiency of executive attention. A number of polymorphisms in dopamine and serotonin genes have been associated specifically with the scores on executive attention (Green et al. 2008). This work is still just getting started, and reports are conflicting. One reason for the conflict may be that genetic variations are also influenced by environmental factors.

Genetic modulation by environmental factors is perhaps clearest for the dopamine 4 receptor gene (DRD4), which has been associated with the executive network in adult imaging studies (Fan et al. 2003b). Data at 18–20 months showed that quality of parenting interacted with the 7 repeat allele of the DRD4 gene to influence the temperamental dimensions of impulsivity, high-intensity pleasure and activity level, and all components of sensation seeking (Sheese et al. 2007). Parenting made a strong difference for children with the 7 repeat allele in moderating sensation seeking but not for those children without this allele. At 3–4 years of age, the DRD4 gene interaction with parenting was related to children's EC, suggesting that executive attention may be the mechanism for this interaction. One study found that only those children with the 7-repeat of the DRD4 showed the influence of a parent training intervention (Bakermans-Kranenburg et al. 2008), suggesting that the presence of the DRD4 7 repeat allele may make the child more susceptible to environmental influences (Bakermans-Kranenburg & Van IJzendoorn 2011, Belsky & Pluess 2009, Sheese et al. 2007). This joint influence of environment and genetics seems to continue into adulthood (Larsen et al. 2010).

Training

Because parenting and other cultural factors interact with genes to influence behavior, it should be possible to develop specific training methods that can be used to influence underlying brain networks. Two forms of training methods have been used in the literature. One involves practice of a particular attention network. Several such attention training studies have shown improved executive attention function and produced changes in attention-related brain areas (Klingberg 2011, Rueda et al. 2005). The practice of a form of meditation has been used to change the brain state in a way that improves attention, reduces stress, and also improves functional connectivity between the anterior cingulate and the striatum (Tang et al. 2007, 2009).

Evolution

The ACC is a phylogenetically old area of the brain. Comparative anatomical studies point to important differences in the evolution of cingulate connectivity between nonhuman primates and humans. Anatomical studies show great expansion of white matter, which has increased more in recent evolution than has the neocortex itself (Zilles 2005). One type of projection cell called a Von Economo neuron is found only in higher apes and a few other social species, but they are most common in humans. In the human brain, the Von Economo neurons are found only in the anterior cingulate and a related area of the anterior insula (Allman et al. 2005). This neuron is likely important in communication between the cingulate and other brain areas. The two brain areas in which Von Economo neurons are found (cingulate and anterior insula) are also shown to be in close communication during the resting state (Dosenbach et al. 2007). It is not clear, however, if the distribution of Von Economo neurons and the cingulo-opercular network are overlapping or closely juxtaposed (Power et al. 2011). Some evidence indicates that the frequency of this type of neuron increases in human development between infancy and later childhood (Allman et al. 2005). These neurons may provide the rapid and efficient connectivity needed for executive control and may help explain why self-regulation in adult humans can be so much stronger than in other organisms.

FUTURE

It has been exciting for us to see the expansion of work on networks of attention over the past 20 years. We now have the opportunity to go from genes to cells, networks, and behavior and to examine how these relationships change from infancy to old age. In development, the number of active control systems increases and their influence changes.

Although much has been learned, many questions remain unanswered. We are hopeful that the study of attention will continue to provide greater understanding of how control develops typically and in pathology (Posner 2012a, Posner et al. 2011) and will provide promising leads for translating basic research into interventions to aid children and families.

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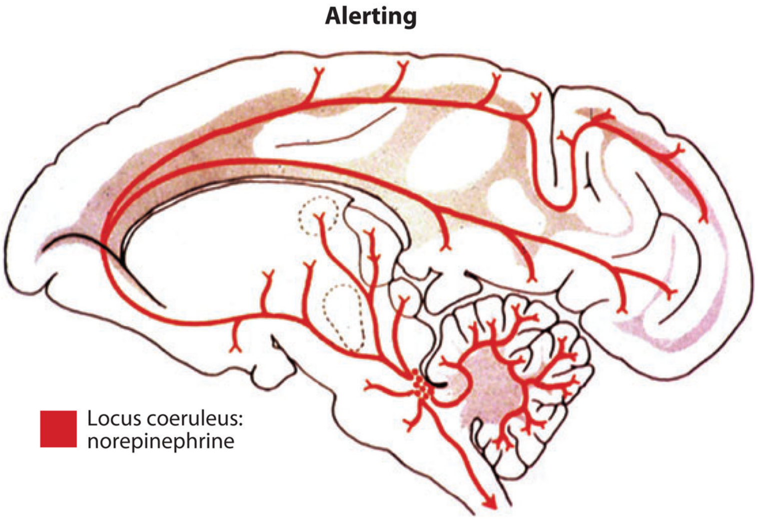

Figure 1.

The locus coeruleus projections of the alerting system shown on a macaque brain. The diffuse connections interact with other, more strongly localized systems. The alerting system also includes regions of the frontal and parietal cortices (not shown). Reproduced from Aston-Jones & Cohen (2005).

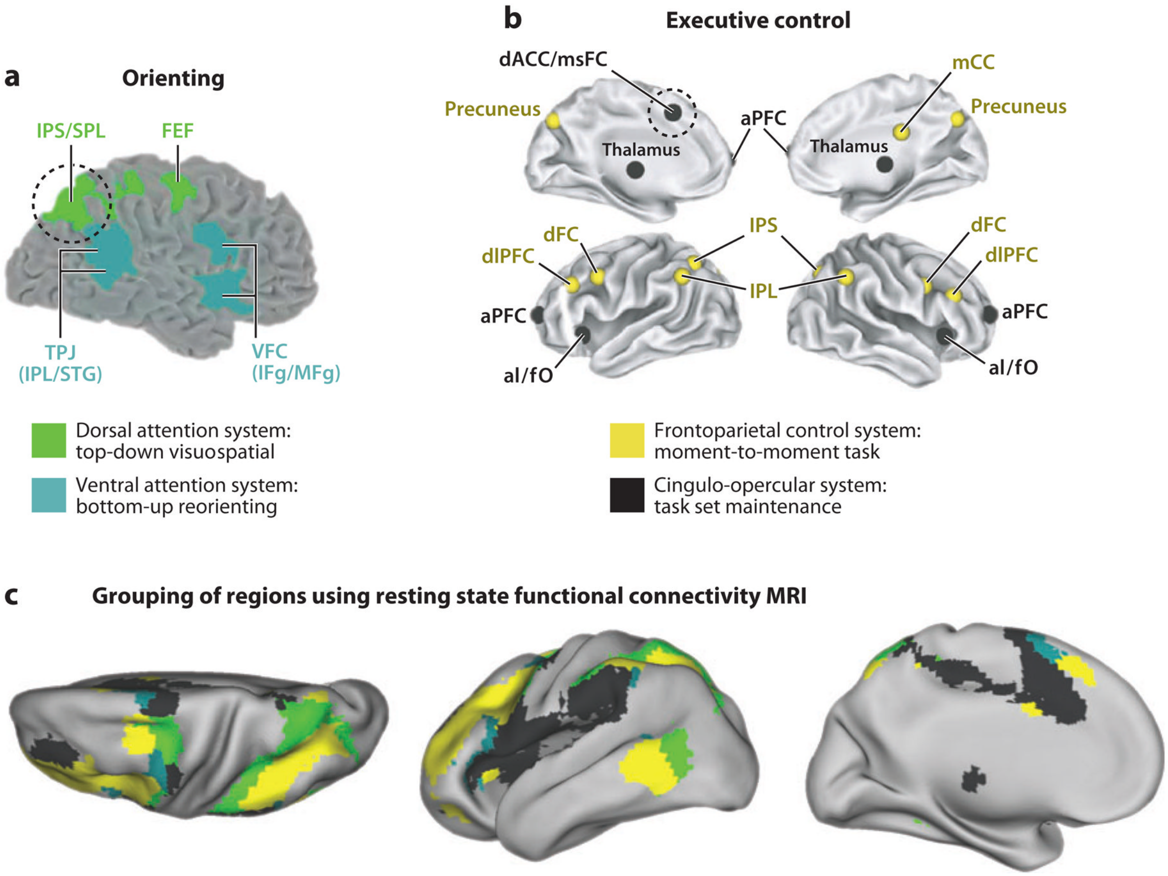

Figure 2.

(*a*) The dorsal and ventral orienting networks (after Corbetta & Shulman 2002). The dorsal attention network (*light green*) consists of frontal eye fields (FEF) and the intraparietal sulcus/superior parietal lobe (IPS/SPL). The ventral attention network (*teal*) consists of regions in the temporoparietal junction (TPJ) and the ventral frontal cortex (VFC). (*b*) Two networks of the executive control system. The circled region indicates the original member of the executive control system from Posner & Petersen (1990). The remaining regions come from the elaboration of the original cingulo-opercular system (*black*) and the addition of the frontoparietal system (*yellow*) (adapted from Dosenbach et al. 2007). (*c*) Resting-state correlation reflecting separate control systems. The figure illustrates three views of the brain (*left*, dorsal view; *middle*, tilted lateral view; *right*, medial view). These separable resting networks are consistent with the distinctions based on functional criteria exhibited in panels *a* and *b*: dorsal attention (*green*), ventral attention (*teal*), cingulo-opercular (*black*), frontoparietal (*yellow*) (adapted from Power et al. 2011).

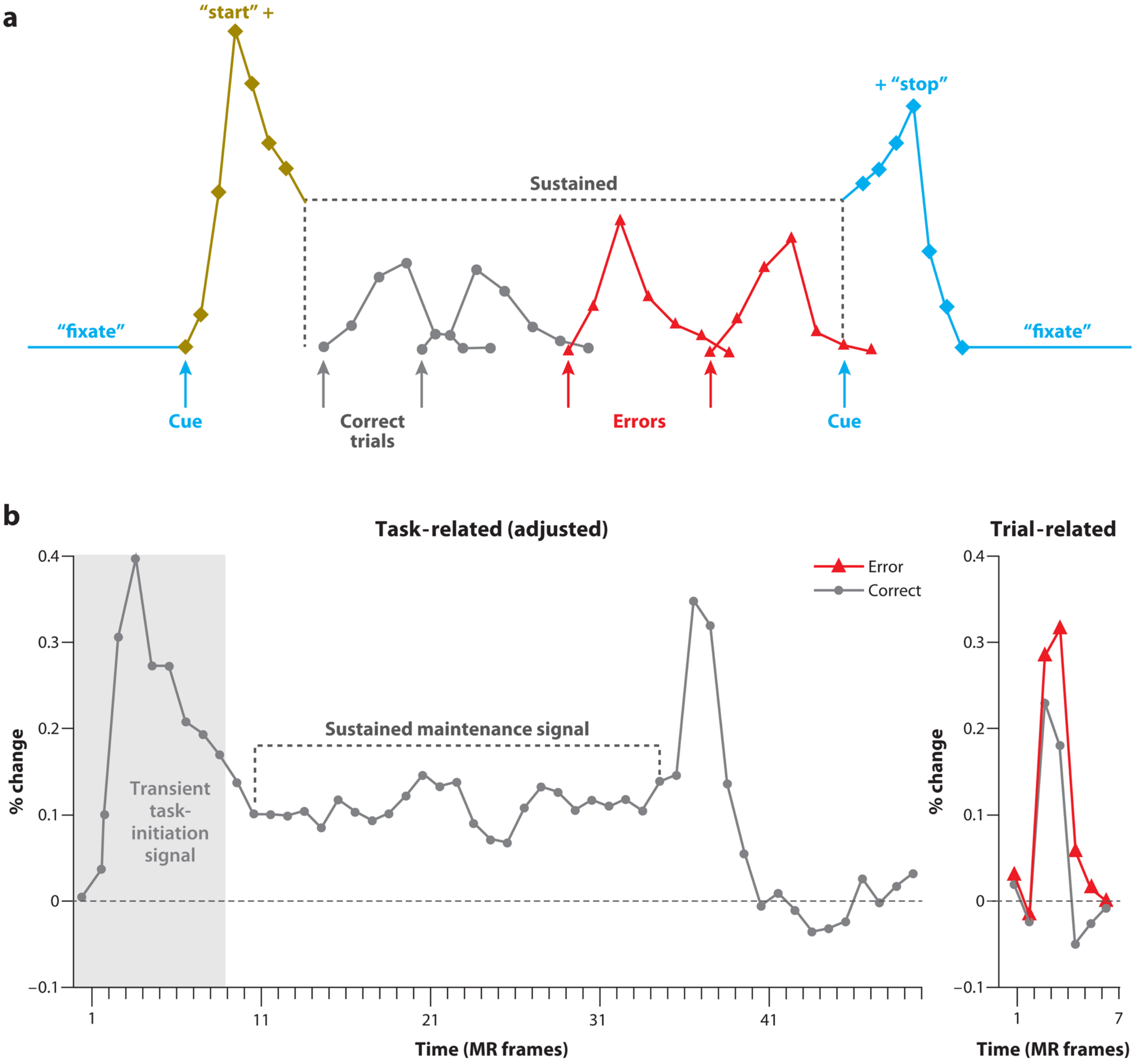

Figure 3.

Executive control signals. The top panel shows three putative executive control signals: a task initiation signal in yellow, a task-maintenance signal in red, and activity related to correct (*black*) and error (*blue*) trials (adapted from Dosenbach et al. 2006). Regions showing differences in error versus correct trials are considered to be computing or receiving performance feedback. The bottom figure shows activity in the left anterior insula during a task that contains all the putative signals (plus a transient transition signal at the end of the block of trials). MR, magnetic resonance.