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IMAGING ATTENTION NETWORKS[1]

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Abstract

The study of attention has largely been about how to select among the various sensory events but also involves the selection among conflicting actions. Prior to the late 1980s, locating bottlenecks between sensory input and response dominated these studies, a different view was that attentional limits involved the importance of maintaining behavioral coherence rather than resulting from a bottleneck. In both cases ideas of resource limits taken over from economics were important. Early evidence relating to the anatomy of attention came from neurological investigations of lesioned patients, but the major impetus for the anatomical approach came from neuroimaging studies that provided evidence of brain networks related to orienting to sensory events and control of response tendencies. The presence of a functional anatomy has supported studies of the development of attention networks and the role of neuromodulators and genetic poymorphisms in their construction. Together these developments have enhanced our understanding of attention and paved the way for significant applications to education, pathology and prevention of mental illness.

Attention is one of the largest topics in the field of neuroimaging and perhaps one in which there has been most consensus. The sheer number of studies in this area makes a review of individual studies difficult and although there is much agreement about the brain areas involved in attention the meaning of these activations is the subject of controversy. This paper first briefly reviews the concept of attention prior to the advent of neuroimaging. Neuroimaging transformed theoretical ideas about the limits of attention into issues concerning the anatomical areas involved. The functional anatomy of attention began with areas of brain activation and only later came the evidence of functional and structural connectivity. The next section of this paper deals with this current state of attention networks based on neuroimaging studies. The final section of this paper points to the future of attention studies within the general framework created by neuroimaging.

ATTENTON BEFORE IMAGING

The study of attention goes back at least to the effort of Sir William Hamilton in 1859 to determine how many items a person may be conscious of at one time (see Woodworth,1938 for a review). The development of experimental psychology in Germany in the late 1800s led to many experiments on attention. However, since psychology at that time was defined

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as the science of conscious mental life only what could be consciously reported was considered. Modern neuroscience looks at aspects of brain activity the boosts or reduces signal strength without regard to whether the person or animal is aware of this activity or not.

Physiology of attention

By the middle of the 20th century psychology was identified with behavior and specific studies of the physiology of attention began with the finding of Moruzzi and Magoun (1949) that lesions of the reticular systems of the midbrain resulting in comatose animals. They argued that what they called the reticular activating system was necessary to maintain alertness. Over the years the study of brain activation and alertness became more specific with the discovery the midbrain chemical systems that together modulated the cortex.

In 1965 Sutton et al (1965) reported that surprising or unexpected events of the type that might capture ones attention produced a strong positive wave recorded from scalp electrodes called the P300. At about the same time Grey Walter (1964) showed that warning signals produced a slow DC shift in the scalp recorded electrical activity that he called the contingent negative variation. Nearly fifty years later these slow wave shifts in the electrical signal were related to the BOLD signal recorded from fMRI (Raichle, 2009).

Hubel and Wiesel (1968) used microelectrodes to probe the structure of the visual system. Before this method could be applied to attention, however, it was necessary to adapt the microelectrode technique to alert animals. This was accomplished in the early 1970s and applied by Mountcastle (1978) and Wurtz, Goldberg, and Robinson (1980) to examine mechanisms of visual attention in the superior colliculus and parietal lobe. Their findings suggested the importance of both of these areas to a shift of visual attention. It had been known for many years that patients with lesions of the right parietal lobe could suffer from a profound neglect of space opposite the lesion. The findings of “attention related cells” in the posterior parietal lobe of alert monkeys suggested that these cells might be responsible for the clinical syndrome of neglect.

An impressive result from the microelectrode work was that the time course of parietal cell activity seemed to follow a visual stimulus by 80-100 milliseconds. Beginning in the 1970s, Hillyard (see Hillyard, Di Russo & Martinez, 2004 for a summary) and other investigators explored the use of scalp electrodes to examine time differences in neural activity between attended and unattended visual locations. They found that early parts of the visual ERP showed changes due to attention starting at about 100 milliseconds after input. These findings showed likely convergence of the latency of psychological processes as measured by ERPs in human subjects and cellular processes measured in alert monkeys. These results were an important development for mental chronometry (i.e. the study of the time course of information processing in the human brain) because they suggested that scalp recordings could accurately reflect the underlying temporal structure of brain activity.

Models

Before the imaging era began, successive metaphors sought an understanding of the many behavioral experiments used to study attention. Broadbent (1958) summarized experiments presenting separate messages simultaneously to the two ears by arguing that attention served as a filter which allowed only information from one ear to be processed while information on the other ear was stored in a sensory store. This simple model was modified by Treisman (1969) who using simultaneous visual and auditory messages and argued for attenuation of one while the other was selected. Kahneman (1973) viewed attention as a resource which could be allocated to various inputs until reaching its limit. Allport (1985) argued against the

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bottleneck or limited capacity idea embodied in all of the previous models by suggesting that the apparent limits on attention were in the service of preserving a coherent output that would follow that person's goals rather than being driven by each input. These varied metaphors raised issues such as how early in time and in the processing stream could attention select input and what was the fate of non attended information.

The most important development in model building appeared in volumes that in 1986 and presented a parallel processing framework for the summarization and expansion of empricial results in all areas of cognition including attention (Rumelhart & McClelland, 1986). These connectionist models were inspired by the idea of connecting neurons, but they lacked any clear idea of the organization of the nervous system. The major initial contribution of these models were to language processing and in particular to how every letter of a word was more visible than the same letter in isolation a result (Reicher, 1962) which appeared to many people raised with serial models of information processing as a paradox. By allow all the letters to activate word tokens in parallel and to feedback to the letter level to reinforce initial activation these connectionist models could account for the behavioral data. While the initial application was to word processing these models were also applied to attention (Cohen, Romero, Servan-Schreiver & Farah, 1994).

Lesions

The effort to connect the empirical models arising from cognitive studies with the cellular studies of attention led to the development of a very simple task to the time course of attention shifts in an otherwise empty field (Posner, 1980). This task required the person to press a single key to a small target. Before the target occurred, a cue was presented which on 80% of the trials indicated where the target would occur (valid cue) and on 20% indicated the position opposite the target (invalid cue). The cue could either occur at the location of the target (exogenous cue) or could be a central arrow (endogenous cue). Reaction times were faster when the person was correctly cued that on invalid trials. Since eye movements were monitored and not allowed and there was only one key to press on all trials the difference in RT between valid and invalid trials it was argued was due to a covert shift of attention.

Mountcastle's cellular work had been aimed at the parietal lobe because patients with lesions there on the right side showed neglect of the side of space opposite the lesion. It had been reported that patients with lesions of the parietal lobe could make same-different judgments concerning objects that they were unable to report consciously (Volpe, LeDoux, & Gazzaniga, 1979). It was also possible to follow this result in more analytic cognitive studies. What did a right parietal lesion do that made access to material on the left side of space difficult or impossible for consciousness and yet still left the information available for other judgments?

This puzzle was partially answered by the systematic study of patients with lesions in various locations in the parietal lobe, the pulvinar, and the colliculus. Patients with these lesions all tended to show neglect of the side of space opposite the lesion. But in a detailed cognitive analysis it became clear that their deficits were in different specific mental operations involved in shifting attention (Posner, 1988). These studies supported a limited form of brain localization.

The hypothesis that arose from early studies of neglect was that different brain areas executed individual mental operations or computations such as disengaging from the current focus of attention (parietal lobe), moving or changing the focus of attention (colliculus), and engaging the subsequent target (pulvinar). If this hypothesis were even partly right, it might explain why Lashley thought the whole brain was involved in mental tasks. Perhaps it's not

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the whole brain's activity, but instead a widely dispersed network of quite localized neural areas.

More recent studies of lesioned patients showing neglect using fMRI methods have partly confirmed and greatly elaborated this idea (Corbetta & Shulman, 2011). Lesions of the right temporal parietal junction seem to be central to showing neglect. However, the ventral part of the orienting network, which contains priority maps of visual locations (Bisley & Goldberg, 2010) also behaves abnormally in these patients even when the lesion does not extend into the more ventral part of the orienting network. The temporal parietal junction on the right side seems critical to breaking attention to a currently attended location so that reorienting can take place.

NEUROIMAGING OF ATTENTION

Orienting of attention

Many visual tasks involve covert or overt shifts of attention within the visual field. These tasks are often more complicated that covert orienting task described above, but they can be viewed as involving the same mechanisms. Hillyard and his colleagues (2004) have demonstrated that When one attends to a location information coming from that location shows an amplified electrical signal that includes an early positive wave (at about 100 millisec called P1) and a subsequent negative wave (N1). This signature of selection by attention has been found for orienting with and without eye movements and in cueing and visual search tasks.

Enhancements due to attention were found with cues to other features than location such as color and form but these were somewhat later in time and involved a sustained increase in the negativity related to N2 sometimes called the processing negativity. An early imaging study using positron emission tomography showed clearly that these enhancement occurred in prestriate areas of the visual system. Studies using event related fMRI together with EEG showed that P1 and N1 attention effects arose from prestriate areas of the visual system

The shift of attention often occurs prior to the occurrence of the target and event related fMRI results suggest that there is a change in the BOLD signal even before the target is presented which then enhances the perception of the target when it occurs. These enhancements involve not only faster responses but also changes improved sensory information (Montagna, Pestili & Carrasco, 2009). One prominent theory that has arisen from these preparatory changes emphasizes the competition between sensory stimuli within various sensory and views attention as biasing this competition toward the cued target (Desimone & Duncan, 1995).

In series of experiment using the cueing methodology and event related fMRI Corbetta and Shulman (2002) were able to show two brain systems related to orienting to external stimuli. A more dorsal system including the frontal eye fields and the inter parietal sulcus followed 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 temporal parietal junction and was identified with an interrupt signal that allowed the switch. The more ventral network including the temporal parietal junction seemed to be ore active following the target and was thus identified as part of a more ventral network responsive to sensory events. There does seem to be a remarkable consensus among researchers of the major nodes of the network involved in orienting of attention to sensory events including spatial cuing studies and visual search (Hillyard. et al 2004; Wright & Ward, 2008).

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

How are the sources of the orienting network described above able to 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 signal arriving in sensory specific areas – for vision, in the primary visual cortex and extrastriate areas moving forward toward the anterior temporal lobe. It appears that this remote influence involves synchronization between activity in the more dorsal attention areas and the more ventral visual areas (Wolmsdorf et al 2007). The synchronization apparently leads to greater sensitivity in the visual system, allowing increased response to targets there and thus improved priority for processing them.

Perhaps the most influential theory of visual orienting in complex scenes is the Feature Integration Theory (FIT) (Treisman & Galade, 1988). When a target is defined by a single feature which distinguishes it from the background it will pop out and thus is without any attentional limit. When, however, the target is defined by a conjunction (e.g. a red triangle with a background of red squares and blue triangles) the search time increases with number of items in the field. To summarize these finding Treisman postulated a map of features. When the target differs from non targets by a single feature the targets requires no search, but conjunctions require a serial search by a mechanism similar to that described above. Treisman predicted that and found that outside the limited attentional system illusory conjunction could be found in which subjects would report the presence of, for example blue square. There have been many disputes about FIT, but most supplement the idea. For example, Wolfe (2007) provided a Guided Search Theory (GST) which deals with expectations activating particular aspects of a central salience map. Many of the ideas FIT and GST are compatible with cellular studies defining visual features and suggesting the presence of priority maps within the parietal cortex (Bisley & Goldberg, 2010).

Cellular studies conducted within visual areas suggest that as items are added to a visual scene they tend to inhibit the overall firing rate of cell responding to their presence. What attention to a target appears to do is to reduce the influence of this competition. This idea was important in the development of biased competition theory (Desimone & Duncan, 1995). This theory sees attention as arising out of the 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 BOLD response and that the overall BOLD activity is reduced through competition.

An interesting feature of visual scenes is that we have the belief that we are aware of all of the items within the scene. However, this appears to be an illusion which arises because attention can be summoned so efficiently within a complex scene to any change that is accompanied by luminance or motion cues (Rensink, O’Regan & Clark, 1997). When these cues are eliminated quite radical changes can occur within the science outside of the current focus of attention which are completely missed. Thus attention must play a very critical role in the rapid assimilation of information from out sensory world.

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Many studies of orienting using fMRI have shown that beyond the orienting network, there is also activity to be found in the other brain areas. For example, in one study the anterior cingulate and midfrontal cortex become active when an unexpected novel target is presented (Shulman et al 2009). The cingulate is often active during cognitive tasks. While many orienting and visual search tasks show cingulate activity many do not. Because the cingulate is activated by pain and reward it has often been thought to be part of networks exclusively involved in these tasks, but of course reward and pain information is important in adjusting behavior to reflect current goals. We have argued the the cingulate is part of an executive attention network involved in controlling other brain networks to reflect current goals (Posner et al 2007). In this sense the executive network is tied to attention because it deals with the problem of which of many active responses are selected. Below we discuss the links between this executive network and issues of self regulation and control.

Attention and Self Regulation

An important idea about the role of the anterior cingulate in behavior is to suppose it is part of a neural network related to the resolution of conflict (Botvinnick, et al 2001). This network might include areas of the prefrontal cortex, anterior insula and basal ganglia as well. There is a great deal of evidence support the idea from imaging of conflict tasks, but this paper tries to view the ability to resolve conflict among responses as part of a more general systems to regulate competing networks (Posner et al 2007). This more general idea rests in part on developmental studies using fMRI.

A major breakthrough in the use of fMRI to study human development has arisen through the study of brain connectivity at rest. While much has been learned from the study of tasks appropriate to infants and young children it is very difficult to design a task that is appropriate and performed with similar strategies and success over a wide range of ages.

A number of studies have examined the brain activity of infants and young children at rest using fMRI (Fair et al., 2009, 2011; Gao et al., 2009). The results to date have shown evidence of sparse connectivity between brain structures during infancy and a strong increase in long range connectivity at 2 years (Gao et al., 2009) and later (Fair et al., 2007; 2009). In studies of neonates, the parietal areas, prominent in the orienting of attention network, show strong connectivity to lateral and medial frontal areas. By age 2, the anterior cingulate, which has been implicated in self regulation, shows stronger connections to frontal areas and to lateral parietal areas. In work with older children and adolescents (Fair et al., 2009), these tendencies continue and the ACC becomes increasingly differentiated from the orienting network as one approaches adulthood. Fair 2011 says

> “the data suggested that there might be at least two control networks functioning in parallel. Based on the differences in their functional connectivity and activation profiles we suggested that each network likely exerts distinct types of control on differing temporal scales. The fronto-parietal network was proposed to be important for rapidly adaptive control and to work on a shorter timescale. The cingulo-opercular network was thought to be important for more stable set-maintenance, and to operate on a longer timescale. Since this initial work there have now been several reports supporting this framework”

Note that the frontal parietal network corresponds to the Orienting network discussed above, while the cingulo-opercular network corresponds to what has been called the executive network involved in resolving conflict. These findings suggest that control structures related to executive attention and effortful control may be present in infancy, but do not exercise their full control over other networks until longer connections are formed later in childhood. Indeed, the connections suggest that initially the ACC has stronger connections to the orienting network and only later becomes differentiated from it. The stronger and earlier

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connections of the parietal areas suggest that in infancy and childhood the orienting network may play a central role in control that is later associated with the ACC. Error detection activates the mid-frontal and/or cingulate areas at 7 months (Berger, Tzur & Posner, 2006), although the ability to infant to take action based on errors seems not be present until 3-4 years of age (Jones, Rothbart & Posner, 2003). These findings suggest that the role of the ACC and other executive control areas increases as long connections with other areas develop.

The ACC is a phylogenetically old area of the brain. Comparative anatomical studies point to important differences in the evolution of cingulate connectivity between non-human 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 Von Economo neuron is found only in the anterior cingulate and a related area of the anterior insula (Allman, Watson, Tetreault, and Hakeem, 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 during the resting state (Dosenbach, Fair, Miezin, Cohen, et al, 2007). Moreover, there is some evidence that the frequency of this type of neuron also increases in development between infancy and later childhood (Allman, et al, 2005). These neurons may provide the rapid and efficient connectivity needed for executive control and help explain why self-regulation in adult humans can be so much stronger than in other organisms.

Individual Differences in Network Efficiency—Everyone has the attention networks described above. However, there are also individual differences in the efficiency of all brain networks. For example, the use of IQ is widespread as a measure of individual intellectual functioning. Fluid intelligence refers to the ability to solve difficult and often unfamiliar problems. Duncan and associates (2000) have shown that a brain network involving anterior cingulate, prefrontal areas and parietal areas is activated by tasks that require fluid intelligence in comparison with similar tasks which do not. It seems likely that this common network differs among people with those with higher levels of general intelligence showing more efficient activation of this network during problem solving.

The Attention Network Test (ANT) has been used to examine the efficiency of three brain networks underlying attention: alerting, orienting and executive attention (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. Reaction times for the separate conditions are subtracted, providing three measures that represent the efficiency of the individual in alerting, orienting and executive networks. In one sample of 40 normal adults (Fan et al 2002) each of these measure to were reliable over a repeated presentation. In addition, there were no significant correlations among the measures. Subsequent work has confirmed the relative independence among networks, while showing that they can interact when conditions are made more difficult or otherwise changed. A study using fMRI showed that the anatomy of these three networks was for the most part independent (Fan et al 2005).

In adults self regulation can be be easily demonstrated by studies that examine either the instruction to control affect or cognition. For example, the instruction to avoid arousal during processing of erotic events (Beauregard, Levesque & Bourgouin, 2001) or to ward off emotion when looking at negative pictures (Ochsner et al, 2001) produces a locus of

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activation in midfrontal and cingulate areas. In cognitive studies, where people are required to select a modality of input, the cingulate shows functional connectivity to the selected sensory system (Crottaz-Herbette & Mennon, 2006). Similarly, when involved with emotional processing the cingulate shows a functional connection to limbic areas (Etkin, Egner, Peraza, Kandel, & Hirsch, 2006). These findings support the role of cingulate areas in the control of cognition and emotion. There is also evidence for anatomical connectivity between the ventral cingulate and limbic areas and the dorsal cingulate, parietal and frontal areas (Beckman, Johanson-Berg & Rushworth, 2009).

Development of executive network—The ability of the child to control conflict in the ANT and other conflict related cognitive task has been shown to correlate with parent reports of the ability of their child to control their behavior (effortful control or EC) at several ages during childhood (Posner et al 2007). This correlation between conflict scores and parental reports of effortful control form one basis for the association between self regulation and executive attention. Effortful control is related to the empathy that children show toward others, their ability to delay an action and to avoid such behaviors as lying or cheating when given the opportunity. High levels of effortful control and the ability to resolve conflict are related to fewer antisocial behaviors such as truancy in adolescents (Rothbart, 2011) These findings show that self regulation, a psychological function crucial for child socialization, can also be studied in terms of specific anatomical areas and their connections by examining the development of the executive network.

Neuromodulators

The networks of attention have also been related to different neuromodulators (Green et al, 2008). The orienting network as discussed above involves areas of the inferior and superior parietal lobe and the frontal eye fields. Cholinergic systems arising in the basal forebrain play a critical role in modulating the orienting network. Lesions of the basal forebrain in monkeys interfere with orienting of attention (Voytko, et al.,1994). However, it appears that the site of this effect is involves the superior parietal lobe. Davidson & Marrocco (2000) made injections of scopolamine, a cholinergic antagonist, directly into the lateral intra-parietal area of monkeys and found that these injections blocked orienting. The orienting network also involves two other major cortical areas: the temporal parietal junction and the frontal eye fields. When systemic, rather than localized injections of scopolamine were used, they also influenced orienting, but had a smaller effect than local injections into the parietal area. Cholinergic drugs do not affect the ability of a warning signal to improve alerting. Pharmacological studies (Beane & Marrocco, 2004) show that noradrenergic antagonists block the warning effect, but do not influence orienting. Thus, there appears to be a double dissociation, with norepinepherine (NE) involved mainly in the alerting network, and Ach (actylcholine) relating to the orienting network.

The executive network involves brain areas that are rich in dopamine and their function is modulated by dopamine from the ventral tegmental areas (da Silva Alves et al 2011; Williams & Goldman-Rakic, 1998). Human imaging requiring the resolution of conflict, such as the attention network task (ANT) have been shown to activate this area (Fan, Fossella et al, 2003) and individual differences in the extent of this activation have been shown to involve dopamine related genes (Fan, Flonbaum et al 2002).

Genes

The common nature of brain networks argue strongly for the role of genes in their construction. This has led cognitive neuroscience to incorporate data from the growing field of human genetics. One method for doing this relates individual variations in genes (genetic alleles) to aspects of human behavior. Brain activity can serve as an intermediate level for

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relating genes to behavior. As one example, the Attention Network Test (ANT) has been used to examine individual differences in the efficiency of executive attention. A number of dopamine and serotonin genes have been associated specifically with the scores on executive attention (Green et al 2008; Posner, Rothbart & Sheese, 2007).

There is evidence that these genetic associations are modulated by environmental factors. This is perhaps clearest for the Dopamine 4 Receptor Gene (DRD4) which has been associated with the executive network in adult imaging studies (Fan, Fossella et al 2003). Data at 18-20 months found that parental quality interacted with the 7 repeat allele of the DRD4 gene to influence the temperamental dimensions of impulsivity, high intensity pleasure and activity level, measures of sensation seeking (Sheese et al., 2007). Parenting made a strong difference for children with the 7 repeat in moderating sensation seeking. Those with poorer quality parenting were far more impulsive and sensation seeking than those with high quality parenting. Parenting quality made no difference for children without the 7 repeat allele. At 3-4 years the DRD4 gene in interaction with parenting was related to children's effortful control. One study found that only those children with the 7-repeat of the DRD4 showed the influence of a parent training intervention (Bakersman-Krannenburg et al 2008), suggesting that at least some of the genetic effects are directly influenced by parenting. These data have suggested that the DRD4 7 repeat presence may make the child more susceptible to environmental influences7 (Bakersman-Krannenberg & van IJzendoorn, 2011; Belsky & Pleuss, 2009; Sheese et al 2007). The importance of this gene on environment impact seems to continue into adulthood (Larsen et al, 2011).

Since parenting and other culture interact with genes to influence behavior it should be possible to develop specific training methods that can be used to influence underlying brain networks. Several training studies have shown improved executive attention function and changes in brain activity using various practice oriented methods of training (Klingberg, 2011) and training methods designed to change the brain state (see Tang & Posner, 2009).

FUTURE DIRECTIONS

It is extremely difficult to predict the future of new basic findings in the study of attention. It is more possible to indicate current gaps that it would be nice to see filled or places where current knowledge of attention might receive fruitful application. Below we concentrate on these points.

Filling Gaps

The excitement in the field of attention is in relating different levels of analysis including behavioral models, imaging, cellular recording and genetics. There has been progress in doing so, but many gaps remain.

As one example, there are plenty of good examples of brain plasticity, but it would be useful to understand the amount of practice needed to change such fMRI measures as activation, functional connectivity, fractional anisotropy or structural MRI. Is there a strict ordering of these changes or do they differ with brain area or task? Even the exact meaning of these changes remains to be fully understood. Fractional anisotropy can be changed by myelination, but what other actors could influence it? Does increase cortical thickness always relate to improved computation?

It would also be nice to know how shifts in covert attention are related to both microsaccades and to the programming of eye movements. It seems clear that they are related, but to what degree are covert shifts dependent upon programming saccades. The finding of somewhat separate and overlapping populations of cells is one important method

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for studying this question (Thompson, Bisco & Sato, 2005). Further steps might involve cellular studies of the frontal eye fields or more accurate MRI methods that could separate cell populations.

While some gaps are at the cellular or imaging level others involve the links between neural networks and behavior. The beautiful studies of the development of the brains connectivity (Fair et al 2007; 2009) provide insights into brain development, but reveals relatively little about what these changes mean for the behavior of the infant and child.

Important application of research on attention are already starting to occur so it may be easier to predict further development places of educational and mental health applications as discussed below.

Education

Imaging has begun to be applied to training of attentional networks of children prior to starting school. Because the ability to regulate conflict and to delay reward are important predictors of school performance, it seemed plausible that practice might have widespread effects on learning. Several methods improve the ability the executive attention network in preschool children (Diamond, Barnett, Thomas & Munro, 2007; Rueda et al 2005), however, we do not know what the long term effects of this kind of training is on school performance. Similar practice oriented training methods of attention and working memory have been used with older children with ADHD (Klingberg, 2011). The behavioral and neuroimaging methods have pointed to improvement in attention and brain systems with training, but whether or not these methods can be sufficiently powerful to replace drug oriented therapies remains to be studied.

Just as fMRI has involved both the study of specific networks during task performance and the study of brain states during rest so attentional training has involved either the practice methods describe above or methods designed to change the brain state in a way that will improve performance such as is involved in some forms of meditation (Tang & Posner, 2009). Some of these studies have involved short term training random assignment and comprehensive assays of performance. While these studies have been promising in adults they need to be applied to children and followed up for their subsequent influence in school.

Mental illness

The ability to image the human brain has provided new perspectives for neuropsychologists in their efforts to understand, diagnose, and treat damage to the human brain that might occur as the result of stroke, tumor, traumatic injury, degenerative disease, or errors in development. Because mental illness are now seen as involving brain networks, the study of neurological and psychiatric disorder have merged.

Attentional difficulties are a very frequent symptom of different forms of mental illness, ranging from learning disabilities to psychopathology. However, without a real understanding of the neural substrates of attention, there has not been a sufficient basis for systematic efforts to remedy attentional problems. This situation has been changed with the application of our understanding of attentional networks to pathological issues. Viewing attention as an organ system and investigating the underlying neural networks provides a means of classifying disorders that differs from the usual internalizing (e.g. depression) versus externalizing (conduct disorder) classification applied to such disorders. In the section below we consider the relationship between attention networks and some common disorders. Even though in general we do not know whether the attention deficits are the causes or the results of the condition, the attention disorder may illuminate the symptoms and suggest methods of prevention and/or remediation.

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Studies that have used the Attention Network Test (ANT) or similar cognitive tests have been useful in the effort to identify which attention network might be at deficit in different disorder. There is evidence that ADHD may involve a deficit in alerting either alone (Halperin, & Schulz, 2006) or in conjunction with an executive deficit (Johnson et al., 2008). Autism is most frequently seen as a disorder of social communication. Autistic children fail to reference others, and they have deficits in communication. However, a deficit found in cognitive studies of autistic children is a failure to orient, even when non-social cues indicate where in space a likely target will occur. A study using the ANT found that children with Autistic Spectrum Disorders (ASD) showed a significant deficit in orienting but not in other networks. (Townsend, Keehn & Westerfield, 2011).). An early deficit in orienting could by itself be important in communication problems, since communication critically depends on social referencing. It seems unlikely that autism is confined to a general orienting deficit, since many other brain and behavioral abnormalities have been reported in this complex disorder, but the orienting deficit may provide an important clue to treatment.

Since executive attention is related to self regulation in childhood as discussed above it is clearly important in many disorders such as those involving conduct, addiction and antisocial behavior. It is not surprising that executive attention seems to be impaired in many forms of mental illness including Alzheimer’s disease and schizophrenia.

The role of attention in various forms of mental illness and the availability of imaging as a means of examining brain networks prior to and following rehabilitation should provide opportunities for research that could fine-tune both behavioral and pharmacological intervention methods. Genetic analysis should also aid in an understanding of who might benefit from particular forms of therapy. These methods and the analysis of attention networks described in this paper could foster efforts at prevention or treatment of mental disorders.

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Highlights

- attention implemented by anatomical networks
- attention networks involved in self regulation
- genes and environment build attention networks