

Anatomy of Attentional Networks

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Attention is a central theme in psychological science. As with other biological systems, attention has a distinct anatomy that carries out basic psychological functions. Disparate attentional networks correlate with discrete neural circuitry and can be influenced by specific brain injuries, states, and drugs. Accordingly, thinking about attention as an organ system is advantageous for understanding the details of this complex cognitive process. In the context of an influential model of attention, this article introduces the broad notion of attention, then addresses its prominent characteristics, mechanisms, and theories. The presentation emphasizes the role of recent neuroimaging data in outlining the functional neuroanatomy subserving distinct attentional networks. A discussion of pertinent results connects attentional networks with self-regulation, development, and rehabilitation training. *Anat Rec (Part B: New Anat) 281B:21–36, 2004.* © 2004 Wiley-Liss, Inc.

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INTRODUCTION

One of the oldest and most central issues in psychological science, attention is the process of selecting for active processing ideas stored in memory in our minds, or aspects of our physical environment, such as objects. The study of attention has become a huge enterprise; last year alone about 300 articles were published on attention (Fig. 1). Throughout history, many great minds have wrestled with the definition of attention. In 370 B.C., Aristotle regarded attention as a narrowing of the senses. Centuries later, William James (1890) contended that “everyone knows what attention is. It is the taking possession of the mind in clear and vivid form of

one out of what seem several simultaneous objects or trains of thought.” James’ account strongly joins attention with subjective experience. Moreover, James’s addressing of attention both to objects and to “trains of thought” is important for understanding current approaches to sensory orienting and executive control (Driver and Frackowiak, 2001; Fernandez-Duque and Posner, 2001; Fan et al., 2003a,b). However, as outlined below,

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attention in the sense of orienting to sensory objects can actually be involuntary and can occur unconsciously. So attention is not, as the quote from William James implies, the same as being aware (see Table 1 for a list of important terms and definitions in this field of study).

Following a lull in the field during the early 1900s, Donald Broadbent resumed the quest after World War II to discover attentional mechanisms. Ap-

plying formal information theory, Broadbent likened attention to a filter. He proposed that attention was bounded by the amount of information located between parallel sensory systems and a limited-capacity perceptual system (Broadbent, 1958). This view facilitated objective studies of the limitations of the human ability to deal with multiple signals at a time in a variety of practical tasks.

As psychology moved toward the study of cognitive mechanisms, new objective methods allowed for investigation into the processes of selection. For example, studies showed that words could activate their semantic associates without awareness of the word’s identity (i.e., priming). The parallel organization of sensory information extends to semantic processing. The act of selecting a word meaning for active attention appears to suppress the availability of other meanings of the selected item and of competing items. Consequently, attention has since been viewed more as a mechanism for providing priority for motor acts than as a filter or bottleneck. For example, the premotor theory suggests that attention is simply a preparation for response, or a selecting of the goal of an intended action (Rizzolatti et al., 1987). The focus on

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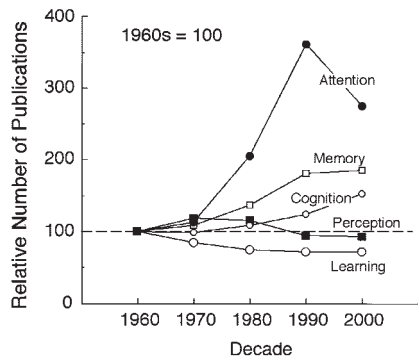


Figure 1. Research into Attention. Relative numbers of publications for each of five key words, normalized to their relative frequencies in the 1960-1969 decade. The 2000 data span only the years 2000 to 2003. The relative frequency values were computed by adding up all the papers that used each of these keywords in 1960-1969 in PubMed and finding the proportion using each keyword. These were the base proportions. The relative proportions were then the proportions in each subsequent decade divided by the original proportions from 1960-1969. From Cavanagh (2003, 2004).

response may explain why attentional systems seem to differ for space that is within reach and space that lies beyond. However, intended actions are probably not the only sources of capacity limits and attentional selection. After all, even when we have no intention to act and passively watch scenes go by (e.g., at the movies), we still select only a subset of the information that reaches the senses. Attention, therefore, was further operationalized as facilitating some kinds of memory and even consciousness.

Other views construe attention in the context of resource limitation/selection. Attentional limits are typically found in unpracticed tasks. However, with practice, most attention-demanding tasks can be rendered attention-independent, or automatized. One example of this phenomenon involves visually searching for a set of letters among other random letters. This task initially demands attention and gives steep slopes of latencies against display size. However, after weeks of practice, the slopes become flat (Spelke et al., 1976; Schneider and Shiffrin, 1977). Another example comes from a demonstration involving two verbal tasks, reading for comprehension and writing to dicta-

tion. These similar and demanding tasks can at first only be done in alternation, but after months of practice can be efficiently combined (Spelke et al., 1976). Given these examples, theories of attentional limits must also account for how these limits can be eliminated (e.g., following practice) when the bottleneck is seemingly bypassed and the correct action is effortlessly performed.

GROSS CHARACTERISTICS OF ATTENTION

Visual attention often serves as a convenient lens to examine the characteristics of attention. Researchers and clinicians have investigated the optics, anatomy, development, pathology, and underlying neural processes of vision, making it the most widely stud-

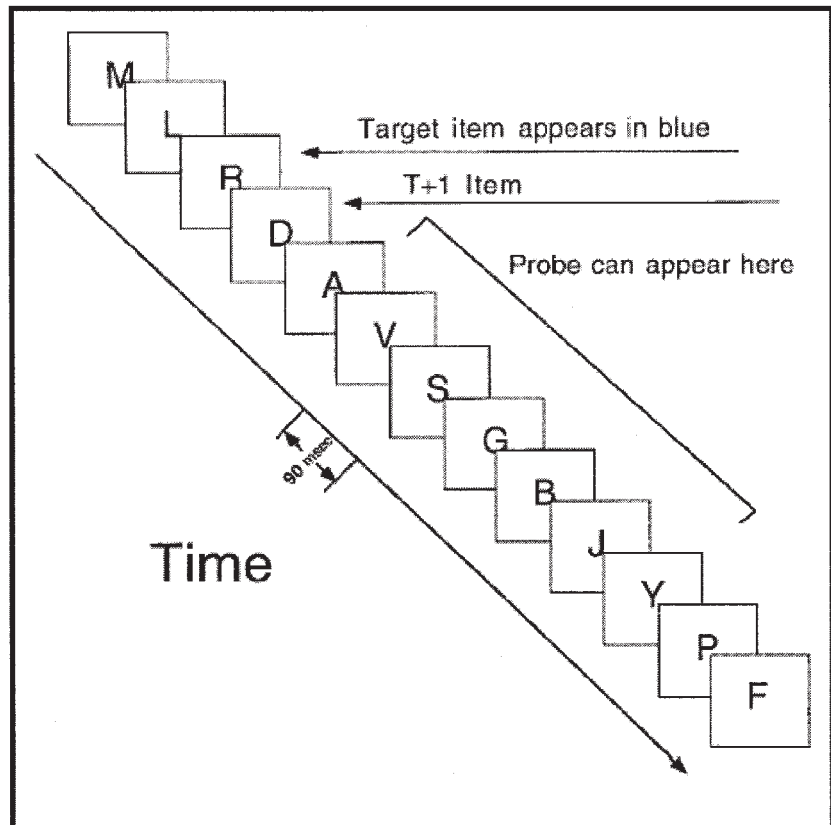
TABLE 1. Terms and definitions related to attentional network research

Foveate	To look at directly so the image being viewed falls on the fovea of the retina
Attention	The mental ability to select stimuli, responses, memories, and thoughts that are behaviorally relevant among a host of others that are behaviorally irrelevant
Attentional networks	Neural circuits subserving attentional processing, which preserve a degree of anatomical and functional independence but interact in many practical situations
Executive network	The mechanism for monitoring and resolving conflict among thoughts, feelings, and responses; an attentional system concerned with such tasks as working memory, planning, switching, and inhibitory control
Orienting	The process of selecting information from sensory input
Alerting	The process of achieving and maintaining a state of high sensitivity to incoming stimuli
Top-down modulation	A downstream effect such as cognitive control, as opposed to a bottom-up effect
Cognitive control	Processes such as conflict resolution, error correction, inhibitory control, planning, and resource allocation
Self-regulation	A key mediator between genetic predisposition, early experience, and adult functioning (e.g., in controlling the reaction to stress, the capacity to maintain focused attention or the ability to interpret mental states both internally and in others)
Neuroimaging	Technologically advanced, often noninvasive, tools for tapping neurophysiological aspects of the behaving brain
Mismatch negativity (MMN)	An electrophysiological manifestation of involuntary preattentive processing occurring when some regularity in the auditory stream is violated by a change (deviant stimulus); the MMN is advantageous with regard to the neural processing of unattended input
Anterior cingulate cortex (ACC)	Part of the brain's limbic system classically related to affect but also active in many studies of cognition; the ACC might be the brain's error detection and correction device part of a circuit involved in a form of attention that serves to regulate both cognitive and emotional processing
Functional magnetic resonance imaging (fMRI)	A noninvasive neuroimaging technique that registers blood flow to functioning areas of the brain in high magnetic fields
Positron emission tomography (PET)	A neuroimaging technique measuring the flow of blood containing radioactive atoms that emit positrons

Box 1. Temporal Aspects of Attention: The Attentional Blink

Temporal allocation of visual attention is often explored using the attentional blink (AB) paradigm (Raymond et al., 1992). AB isolates one aspect of attention allocation and avoids the problem of interpreting results tapping concurrent higher cognitive functions. In the AB, visual attention must be directed to two items in close temporal and spatial proximity. The blink refers to the brief period in which processing of the first target item interferes with processing of a second target (or probe). In a typical AB task, a stream of letters appears in a rapid serial visual presentation while participants identify a target and also determine whether a probe appears later in the same stimulus stream.

A classic example of AB, following Raymond et al. (1992), is to present one blue letter in a rapid visual stream of black letters at the same spatial location (Box 1 Fig. 1). The task is to identify the blue target letter and then detect the presence or absence of a probe letter. Probe detection in this dual-task condition is compared against a baseline condition in which only the probe letter must be detected. Processing of the probe is impaired for up to 600 msec after the target in the dual-task condition (Raymond et al., 1992; Shapiro et al., 1994). This impairment of probe processing disappears after about 700 msec (i.e., probes appearing later than 700 msec following targets can be detected as well as probes appearing in streams requiring no target identification). Notably, detection of probes immediately following the target (i.e., in the $T + 1$ position) is spared relative to detection of probes in subsequent positions. It is as if the item in this position is able to slip



Box 1 Figure 1. The attentional blink paradigm tests attention by overloading it; a list of stimuli is presented very rapidly in succession at the same location on a computer screen. Each item overwrites the last while participants monitor the list using two criteria. For example, the criteria might be to detect the blue letter target and to identify the "B" probe. If the interval of appearance between the target and the probe is greater than about 3/4 of a second, then both are usually reported correctly. However, when the interval between the target and the probe is shorter (e.g., 200–500 msec), the ability to report the probe declines. This decline constitutes the attentional blink, an interval of time when attention is supposedly switching from the first criterion to the second. Adapted with permission from Hollingsworth et al. (2001).

through an attentional "gate" opened by the processing of the target (Raymond et al., 1992). One benefit of this task is that it isolates temporal allocation of attention without introducing the spatial switching component of other visual attentional tasks. Other

advantages of the AB lie in the fact that it avoids the problems of ceiling effects, continuous-performance tests, response inhibition or motor control, and can be effectively used with pathological populations (Hollingsworth et al., 2001).

ied perceptual system. Studying visual attention allows us to explore how we move the attentional "beam" around to various areas of the visual field and change the detail with which we look at any given area. For example, it is possible to look at this page and pay attention to its setup as a whole, or concentrate on specific words and certain letters therein. Paying attention

to single characters permits us to catch typos, glean information about punctuation marks, and even spot minute imperfections on the physical paper. However, at this level of detail, we may miss the bigger idea conveyed in a paragraph. As we shift our focus, we can change the target location of our attention or the size of our attentional field. Many metaphors describe

visual attention: "spotlight," "zoom lens," "gating," and "gradient," along with the common usage of terms such as "attentional gaze" or "attentional focus" (Shalev and Algom, 2000). The notion of a spotlight, which started out as a crude metaphor and has since been taken up as a serious viewpoint to be tested, is a natural derivative of the spatial milieu in which attention is

assumed to operate and relates to the common experience concerning the kind of attention needed for reading versus proofreading. The bulk of the evidence suggests that attention can have an influence quite early in the visual system and scientists are still learning what visual operations attention could potentially influence (Robertson and Garavan, in press). However, it is important to complement the spatial aspects of attention with its temporal limitations (see Box 1).

Given a large visual array of individual features, one can choose either to examine it globally or to investigate its specific features. Using compound stimuli for studying global and local processing, it is possible to study how one can shift back and forth between them by changing the attentional focus (Navon, 2003). For example, certain patients have difficulty examining the local features. These patients usually have damage to the left temporoparietal lobe. Other patients may do well with the local features, but fail to appreciate the overall contour; they usually have damage to the right temporoparietal lobe. Indeed, the parietal lobe tends to emphasize the shifting between local and global stimuli, while the temporal lobe seems to determine whether one can actually examine a local or global feature of the stimulus.

We usually foveate, or look at, exactly the thing in which we are interested, and that process generally relates our attention to where we fixate. However, it is easy to dissociate attention from the fovea. We can cue people to attend to some location in space other than the center of gaze and then show that they are sensitive to information that occurs at the cued location and relatively slow or insensitive to information at the fovea, as measured by a low threshold or fast response time (Posner, 1980). It is believed that these covert shifts in attention are used to select the part of the visual field to which one usually wants to move the eyes because in everyday life, one usually follows covert shifts of attention with an eye movement. Attention to visual elements can also apply to other modalities, such as the auditory system.

When multiple people talk simultaneously, it is sometimes necessary to

select one out of these streams of conversation to follow in detail. We usually do that based on the location of the person: we may visually orient toward the person and/or hone in on their frequency of voice. For example, we can typically separate a male voice from a female voice more easily than we can separate two male voices. Alternatively, we may pay attention to the content of the information by following a story line. When we attend to one stream, the other information coming from conversations around us goes into the background: it is present, but does not reach focal analysis. Data suggest that much of this unattended information is actually processed in subtle and complicated ways (Kihlstrom, 1996). Moreover, unattended information can suddenly become interesting (e.g., when our

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and anatomy.**

name is mentioned), whereby we orient to the new information. These attentional phenomena have been studied experimentally in some detail and will be described next.

ATTENTION AND PERCEPTION

Attention is not a panacea to perception because there is a great deal attention cannot do (Raz et al., 2004b; Raz, 2004a,b). For example, while orienting to a location, attention can give priority to that location (i.e., targets that appear there will be perceived more rapidly and with lower thresholds). However, attention cannot substitute for the acuity provided by the fovea. While the fovea is critical for acuity, the costs in reaction time for an unexpected foveal stimulus are just as great as for an unexpected peripheral event. Thus, visual attention in-

fluences priority or processing preference, but also modulates sensory processing and top-down control (Pessoa et al., 2003; Raz, 2004) and may even affect accommodation (Raz et al., 2004a).

Compared to unattended stimuli, behavioral findings show that reaction time to attended stimuli is usually faster. Neurophysiological data reveal enhancement of electrical activity over extrastriate visual areas by about 90 msec following visual presentation. Although performance may improve on increased attentional investment, great controversy has existed over what orienting attention to a sensory stimulus actually does. The psychophysics literature provides reliable accounts of how visual thresholds correlate with attentional investment. Studies show that improvement in visual acuity is not synonymous with altered thresholds for detection, better performance, or faster reaction times. Whereas acuity requires the resolution of detail, detection thresholds and reaction time can involve the summation of luminance, which might obscure detail (Raz et al., 2004b).

Although investing attention is frequently associated with looking directly at the scene of interest, covert attention is the ability to grant such information priority in processing without eye movement. Researchers have shown that the performance improvement at attended locations results somewhat from an enhanced spatial resolution at the cued location (Yeshurun and Carrasco, 1998, 1999, 2000; Carrasco et al., 2002). Studies exploring the relationship between visual attention and contrast sensitivity show that covert attention not only improves discrimination in a wide variety of visual tasks, but could also increase the rate at which information is processed. Some findings do indicate that contrast sensitivity is greater in the lower versus higher visual meridian. However, most evidence sets limits to the effects of attention on spatial resolution and specifies that certain visual, not attentional, constraints determine aspects of spatial resolution (Talgar and Carrasco, 2002).

ATYPICAL ATTENTION

Biological rhythms affect attentional performance. Diurnal reductions in attention normally occur during the hours of maximum sleepiness, 2:00 a.m. to 7:00 a.m., which coincides with the period of lowest body temperature. Attentional performance is usually enhanced in the evening, when body temperature peaks (Raz, 1999; Manly et al., 2002). During the states of sleep deprivation and sleep, voluntary attention is often markedly attenuated or even absent. However, evidence suggests that certain attentional as well as preattentional mechanisms remain intact albeit unstable (Raz, 1999; Raz and Posner, 2000; Doran et al., 2001; Raz et al., 2001). Dreaming is usually divorced from a sense of controlled awareness. However, purported accounts of lucid dreaming, in which persons dream while knowing that they are dreaming, suggest that some control mechanisms may be available during sleep. Other common anecdotes in support of this concept include the incorporation of ambient sound into the dream content as well as the idea of sensitivity to one's own name.

To investigate information processing in sleep, researchers measure electrical recordings from the scalp using electroencephalography (EEG). By averaging the brain's electrical response potentials to stimuli using a technique called event-related potentials (ERPs), it is possible to examine the processing capability of the sleeping brain. One such component to examine is the mismatch negativity (MMN). The MMN is an electrophysiological manifestation of involuntary preattentive processing in response to oddball stimuli. In a typical MMN paradigm, a deviant auditory stimulus is infrequently interspersed within a sequence of standard auditory stimuli. The MMN is evident in the difference waveform resulting from the subtraction of the ERP elicited by the standard stimulus from that elicited by the novel auditory stimuli (the deviants). The difference waveform, occurring even without attention, normally peaks between 100 and 250 msec from the onset of the deviant event. This value depends on the dimension of deviance and its

magnitude. The MMN presumably indicates a mechanism that compares the current auditory input to the memory traces formed by previous auditory inputs and signals the occurrence of a mismatch (Näätänen, 2003).

In adults, MMN tends to decline during drowsiness and its persistence into adult human sleep is still debated (Atienza et al., 2002). Other EEG components do reflect the brain's reaction to novelty. Although active midbrain inhibition blocks cortical activity in the developed brain, the sleeping infant brain is probably not as capable of blocking and inhibiting information efficiently. Indeed, MMN is obtainable from newborns and young infants and experimental data show that during those early developmental stages, the brain can learn, even during sleep (Cheour et al., 2002).

Two recently developed tools have been particularly valuable in studying attention as an organ system: brain imaging and genomics.

Attention is sometimes associated with hypnosis, a special cognitive state sometimes confused with sleep. Hypnosis has been used clinically for hundreds of years and is primarily a phenomenon involving attentive receptive concentration. Following particular suggestions, highly hypnotizable individuals may experience attentional and perceptual changes, which may not typically occur during common awareness. In a responsive subject, suggestions for perceptual alteration are accompanied by reproducible changes in brain action. For example, the activity of the anterior cingulate cortex (ACC) to painful stimuli or conflict resolution can be modulated by hypnotic suggestion (Rainville et al., 1997; Raz and Shapiro, 2002; Raz, 2004). Interestingly, most children are highly hypnotizable and more easily inducted into hypnosis than are adults.

ATTENTION AND NEUROIMAGING

Two recently developed tools have been particularly valuable in studying attention as an organ system: brain imaging and genomics. Neuroimaging has illuminated the anatomical areas involved in attention, while the Human Genome Project is identifying genes involved in these networks. This article focuses on data concerning the neuroimaging of attention. The genetics of attention and the interaction between the two methodologies are addressed elsewhere (Fossella et al., 2002b; Fan et al., 2003c).

The past 2 decades have ushered in a new era of methodological advances in tools for noninvasive imaging of the living brain. The information gleaned from such advances has identified both anatomical and functional aspects of the neural processes underlying attention (Kastner and Ungerleider, 2000, 2001; Driver and Frackowiak, 2001; Pessoa et al., 2003). Functional neuroimaging methods allow researchers to measure changes in brain activity associated with simultaneous changes in behavior, or in response to a wide variety of stimuli. ERP, functional magnetic resonance imaging (fMRI), magnetoencephalography (MEG), near-infrared spectroscopy (NIRS), positron emission tomography (PET), and single photon emission computed tomography (SPECT) all measure aspects of physiological change in brain activity.

Early neuroimaging techniques of the 1970s allowed researchers to record from cells in alert monkeys performing an experimental cognitive task. Data from these assays showed increased firing rates for cells in a number of brain regions when the monkeys paid attention compared to when they did not (Wurtz and Goldberg, 1972). These efforts directly related to studies of other aspects of attention, such as research carried out in the 1960s to decipher the mechanism of brain information processing (e.g., Broadbent). Since the 1980s, the study of patients with focal brain lesions and ERPs has established links between the brain areas showing selective enhancement and specific aspects of information processing. Recently, neuroimaging methods were

developed that expanded the types of attention that could be studied physiologically. Some of these findings began to influence computational models of attention (LaBerge, 1994).

Psychological studies have elucidated the pertinent questions about attention. These studies created a substantial number of experimental paradigms, including dichotic listening, visual search, dual-task performance, flanker tasks, rapid serial visual presentation, and negative priming. Through these models, researchers hoped to capture the range of phenomena encompassed by attention under the controlled conditions required by scientific scrutiny. Converging evidence is vital to such analysis as scientists test hypotheses in a variety of different ways so that artifacts of one method are circumvented by another. Confidence in the conclusions increases with replications and the systematic dismissal of potential and lingering caveats. Since inferences are necessarily indirect (e.g., observation of behavior or measurement of brain activations), by putting them together, one further constrains the proposed theories.

While the psychology of attention has furnished a number of interesting results regarding the limits of performance and of unconscious processing, there was no agreement on whether attention involved separate mechanisms from those used to process data, nor did psychological studies analyze the neural mechanisms of attention. Furthermore, because observable responses are needed as evidence, purely psychological studies are limited in their ability to determine how much information is processed concerning unattended messages. Fortunately, brain imaging allows monitoring of incidental and involuntary processing of unattended stimuli. Insights into the neural systems underlying attention, therefore, markedly benefited from experimental paradigms involving selection of sensory information coupled with the technological innovation of imaging the living brain.

Brain imaging, including data from implanted electrodes in both human and nonhuman primates, has forged an impressive link between psychology and neuroscience (Posner,

2004b). Neuroimaging data have confirmed earlier notions that attention is not a unitary concept and that the human brain likely entertains several attentional systems of different though interrelated functions (Posner and Petersen, 1990). Indeed, for the last 15–20 years, brain imaging has been examining questions of attention and many other cognitive tasks. Major results of this research can be summarized in three statements (Posner, 2004c). One, networks of neural areas, often widely scattered over the brain, but not involving the whole brain, compute cognitive and emotional tasks. Each node of the network computes a different aspect and together the networks orchestrate the whole task. Two, some networks are involved in the control of other networks. These attentional networks are involved in the selection and control of networks that process sensory in-

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formation and information from memory. Three, these networks change with development, learning, brain injury, and pathology.

Given the increased description of attentional networks in recent years, we can now use these networks as model systems for the exploration of symptoms arising from various forms of pathology (Berger and Posner, 2000). Current research has demonstrated that distinct brain areas indeed mediate different attentional processes and thus it is now possible to examine selective attention as an organ system with its own functional anatomy, circuitry, and cellular structure (Posner and Fan, 2004). Although still incomplete, this information has illuminated important questions in cognitive science and has provided insights into neurological and psychiatric disorders of both children and adults. Converging data now point out

that attention enables the exercise of voluntary control over thoughts, feelings, and actions as a means of self-regulation (Raz, 2004) in adulthood and throughout development (Posner and Rothbart, 1998, 2000; Bronson, 2000; Rothbart et al., 2004). Variations in the operational efficiency of these attentional systems explain differences in self-regulation and emotional control and promise to help describe mechanisms of volition and sustained effort (Rueda et al., 2004b, in press). In a way, this network approach owes a lot to the work carried out about 50 years ago by Donald O. Hebb, who outlined in his cell-assembly theory the ensemble of areas in the brain that might be involved in processing cognitive and emotional tasks (Posner and Rothbart, in press).

DIFFERENT TYPES OF ATTENTION

Attention does not imply a singular mechanism; rather, it is a complex system presiding over a number of distinct neuronal circuits. This understanding comes from combining data gathered using various neuroimaging techniques. Early PET data show that different attributes such as color, motion, and shape are processed by at least partially separate systems (Corbetta et al., 1991a, 1991b). Additionally, a recent review of fMRI results reveals a distributed system of brain regions that control attention (Fan et al., 2003a; Pessoa et al., 2003). Accordingly, researchers have formulated experimental paradigms that considerably shape our understanding of attention. More recently, the notion of attention has been extended to the control of action, thought, and affect both in adults and across development (Posner and Rothbart, 1998, 2000; Rueda et al., 2002; Rothbart et al., 2003, 2004; Rueda et al., 2004a, 2004b, in press).

Three largely disparate attentional control systems—select, orient, and alert—have been identified. Although the three systems interact in many practical contexts, the operations of these attentional networks have a certain degree of functional and anatomical independence. Whereas the select system involves choosing among conflicting actions, orient refers to a point of reference to sensory objects, and

alert involves changes in the internal state in preparation for perceiving a stimulus. Insult to each of these distinct attentional circuits, irrespective of the source, produces dissimilar neuropsychological deficits. Correlating the etiologies of such injuries with subsequent changes in behavior and cognition allows us to extend the role of attentional neuroimaging possibly into rehabilitation (Robertson, 1999; Fan et al., 2003b; Posner and Fan, 2004; Rueda et al., in press). Researchers have illuminated the neurochemical substrates of these attentional networks and detailed analyses are now emerging for these orthogonal sensory systems (Raz and Shapiro, 2002; Fan et al., 2003b; Posner, 2004a).

Neuroimaging findings have shown activation of frontal areas associated with paying attention in the context of strong mental effort. For example, when experimental tasks appear to involve significant exertion during target detection or conflict resolution, the area of the ACC is consistently activated. Thus, the select network is a higher-level metacognitive attentional system related to the subjective impression of mental effort (Fernandez-Duque et al., 2000a, 2000b). This form of supervisory or executive attention comprises the mechanisms for monitoring and resolving conflict among thoughts, feelings, and responses. Therefore, this attentional system is concerned with such tasks as working memory, planning, switching, and inhibitory control. Since frontal patients are less able to implement a set of instructed goals, the orbital frontal area is probably important for this executive faculty (Duncan et al., 1996).

Visual orienting is the process of selecting information from sensory input. Orienting of attention toward visual objects can be either triggered by the stimuli (e.g., by brief presentations) or shifted as a result of voluntary control. Orienting has thus become a vehicle for separating automatic from voluntary mechanisms. Early PET results have underlined the importance of the parietal area together with thalamic and mid-brain areas for visual orienting. The orienting network has been used to understand the effects of lesions that produce neglect of sensory informa-

tion either by brain damage or by restricting transmitter input. Likewise, frontal attentional networks have provided similar understanding of pathologies at higher levels of cognition. For example, evidence exists relating frontal networks to attention deficit hyperactivity disorder (ADHD) (Berger and Posner, 2000). Recent research has linked the cholinergic system to orienting (Beane and Marrocco, 2004).

The alert, or vigilant, system functions to achieve and maintain a state of high sensitivity to incoming stimuli. The process of acquiring and maintaining alertness in the face of prolonged dull tasks has been an area of vigorous research. Recent reports have suggested some of the anatomy involved in how arousal, alertness, and vigilance affect performance

Alerting involves a change in the internal state in preparation for perceiving a stimulus. The alert state is critical for optimal performance in tasks involving higher cognitive functions.

(Robertson and Garavan, in press). They also highlight the importance of norepinephrine modulation in the alerting that follows warning signals (Witte and Marrocco, 1997; Witte et al., 1997).

SUBSTRATES OF ATTENTIONAL NETWORKS

Attention can enhance neural processing at multiple levels. As a selective aspect of information processing, attention allows some things to be privileged while others are ignored. Vigorous studies into the modulation of neural responses by attention have revealed that attention can be viewed as a system of anatomical areas carrying out the functions of alerting, orienting, and executive control (Posner and Raichle, 1996; Posner, 2004a). In line with an attentional research agenda

(Posner and Fan, 2004), we have recently devised a simple Attention Network Test (ANT) that can be performed by adults, children, patients, and even nonhuman animals (Fan et al., 2002). The ANT takes about 30 min to administer and provides three numbers that indicate the efficiency of the networks that perform the alert, orient, and conflict-resolution functions. Previous work with this test provided evidence on its reliability, heritability, and the independence of the results (Fan et al., 2001a, 2001b; Fossella et al., 2002a). Recent neuroimaging findings have also used the ANT to probe and assess these distinct attentional networks (Fan et al., 2001a). These behavioral and imaging data suggest that the networks are largely independent and further permit identification of the neuroanatomy subserving these attentional networks (Fig. 2).

Although previous studies have examined areas of the brain involved in various ANT components (Corbetta et al., 2000; Hopfinger et al., 2000), neuroimaging the ANT has illuminated areas involved in carrying out these attentional networks as a whole. fMRI data from the ANT indicate that three largely orthogonal networks relate to components of attention (Fan et al., 2001a). Pharmacological studies have related each of these networks with specific chemical neuromodulators. First, cholinergic systems arising in the basal forebrain play an important role in orienting (Beane and Marrocco, 2004). Second, the norepinephrine system arising in the locus coeruleus of the midbrain functions in alerting (Witte and Marrocco, 1997; Witte et al., 1997; Coull et al., 2001). Third, the ACC and lateral prefrontal cortex are target areas of the mesocortical dopamine system involved in executive attention (Marrocco and Davidson, 1998; Deth et al., 2004; Robbins et al., 2004).

Alerting involves a change in the internal state in preparation for perceiving a stimulus. The alert state is critical for optimal performance in tasks involving higher cognitive functions. Neuroimaging studies have shown activity in the frontal and parietal regions particularly of the right hemisphere when people are required to achieve and maintain the alert state

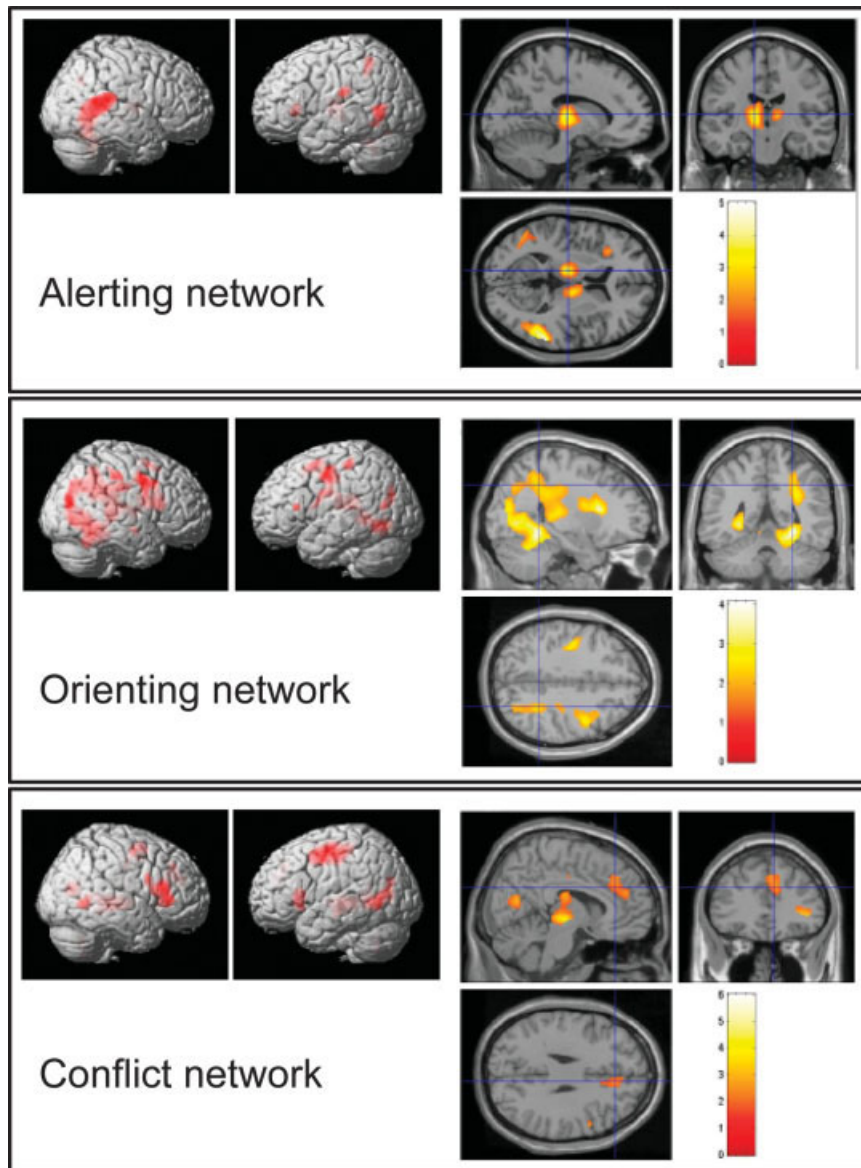


Figure 2. Anatomy of attentional networks. fMRI images collected from 16 healthy adults performing the ANT in a 3 Tesla magnet (Fan et al., 2001). Cross-sectional views of the three attentional networks; the alerting network shows thalamic activation, the orienting network shows parietal activations, and the conflict network shows anterior cingulate cortex activation. First presented at the 2001 Annual Meeting of the Society for Neuroscience, this figure outlines some of the functional anatomy subserving these distinct attentional networks. The color bar shows fMRI signal level (Z-scores) above the 0.05 significance threshold. The novelty of the ANT is that it illuminates the separate attentional networks described in recent literature, all within one relatively short task that can be run with children and animals, as well as deficit populations and adults.

for even a brief period. Thus, lesions of these areas reduce the ability to maintain alertness. Right frontal lesions impair one's ability to sustain attention voluntarily, which produces more errors over time than are found for left frontal patients in tasks involving continuous performance. Right parietal patients have difficulties in both maintaining the alert state and in attentional orienting. Together, these

deficits produce a profound neglect in the visual field opposite the lesion. Alerting is thought to involve the cortical distribution of the brain's norepinephrine system arising in the locus coeruleus of the midbrain.

The orienting network concerns the selection of information from sensory input. Cholinergic systems arising in the basal forebrain play an important role in orienting. The pulvinar, supe-

rior colliculus, superior parietal lobe, and frontal eye fields are often activated in studies of the orienting network. Orienting can be reflexive, as when a sudden target event directs attention to its location, or it can be voluntary, as when a person searches the visual field for a target. Orienting typically involves head and/or eye movements toward the target, as in overt orienting. However, the process can also be covert. A few dorsal brain areas, including the superior parietal lobe and temporoparietal junction, serve as common sources of attention to sensory stimuli. These regions produce effects within a network of areas that depend on modality, such as ventral visual areas in the case of visual input. The strongest evidence for localization of mental operations stems from the area of attentional orienting toward sensory stimuli. A confluence of methods and experimental sophistication has demonstrated how separate brain areas can be invoked to organize a simple attentional shift. There is agreement that orienting of attention to a visual stimulus produces amplification in prestriate regions. This activation affects processing in all subsequent regions, which feeds back to influence processing in the primary visual cortex (V1) and perhaps in the lateral geniculate nucleus of the thalamus.

Executive control of attention involves more complex mental operations both to monitor and resolve conflict between computations occurring in different brain areas. Executive control is most needed in situations involving planning or decision-mak-

Congruent:
 RED, YELLOW, GREEN, BLUE

Neutral:
 LOT, FLOWER, KNIFE, SHIP

Incongruent:
 RED, YELLOW, GREEN, BLUE

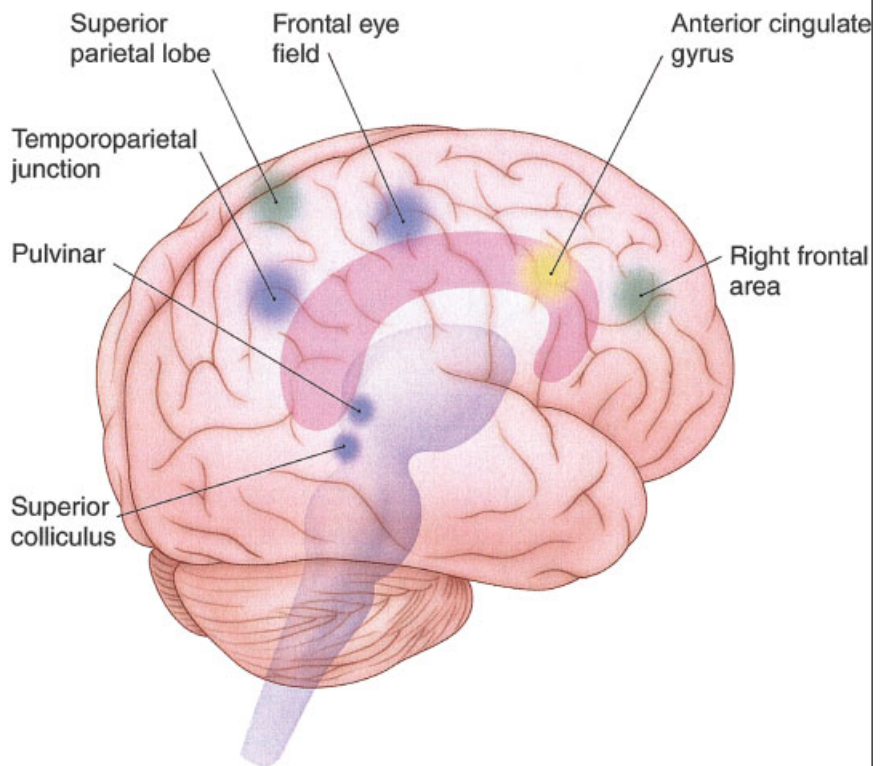
Figure 3. The Stroop effect: an example of selective attention. In responding to the ink color of an incompatible color word, participants are usually much slower and less accurate than in identifying the ink color of a neutral (or congruent) item. This is called the Stroop interference effect and is one of the most robust and well-studied phenomena in attentional research

Box 2. Posnerian Trinity of Attention

By following a trinity proposed by Michael I. Posner (Posner and Petersen, 1990; Posner and Raichle, 1996; Fan et al., 2003b; Posner and Fan, 2004), attentional networks can be construed in terms of, one, obtaining and maintaining the alert state; two, orienting to sensory information; and three, the executive functions involved in resolving conflict between competing areas of the brain that might be simultaneously active. The orienting network relies heavily on parietal systems, including the superior parietal lobe and the temporal parietal junction. It is involved in both orienting to visual information and stimuli in other modalities. The alerting network relies heavily on thalamic areas, locus coeruleus, and cortical areas. The executive attention network relies on the anterior cingulate and lateral areas of the prefrontal cortex (Box 2 Fig. 1).

In a set of influential experiments investigating the neuropharmacology of attention in alert monkeys, Marrocco and Davidson (1998) correlated each brain network with different neuromodulators. These data identified that the orienting network is modulated by the cholinergic system, the alerting network by the norepinephrine system, and the executive network by mainly dopamine systems. Together with Box 2 Figure 2, Box 2 Table 1 depicts the structures involved as the sources of the Posnerian trinity of attention, the sites on which these structures operate, and the neuromodulators they use.

Although the sources of attentional effects are limited to networks, attention can influence any part of the brain, including the brain's primary sensory areas and circuits governing emotions. This influence was nicely demonstrated in a summary of many studies looking at the role of the ACC in the monitoring and resolution of conflict (Bush et al., 2000). The exact mental operations performed by the ACC remain in dispute (Bush, 2004). However, overall the ACC is involved in self-regulation, in which subjects are required to damp down or ward off negative thoughts (Ochsner et al.,



Box 2 Figure 1. A sketch of the functional anatomy of the attentional networks. The pulvinar, superior colliculus, superior parietal lobe, and frontal eye fields are often activated in studies of the orienting network. The temporoparietal junction is active when a target occurs at a novel location. The anterior cingulate gyrus is an important part of the executive network. Right frontal and parietal areas are active when people maintain the alert state. Adapted with permission from Raz and Shapiro (2002).

2002) or even pleasant thoughts (Beauregard et al., 2001). The dorsal part of the ACC, which is involved in cognitive tasks, is distinguishable from the more ventral part, which functions in emotional tasks (Bush et al., 2000; Bush, 2004). Thus, it is reasonable to consider the ACC an important node in the monitoring and resolution of conflict that occurs in emotional and cognitive regulation (Posner, 2004c).

Many of the tasks used to activate the ACC are Stroop-like tasks that require language. However, researchers have developed some language-independent tasks suitable for young children. For example, an adaptation of the Flanker task (Eriksen and Eriksen, 1974) asks a child the direction of a swimming fish that is surrounded by other fish swimming in the same or

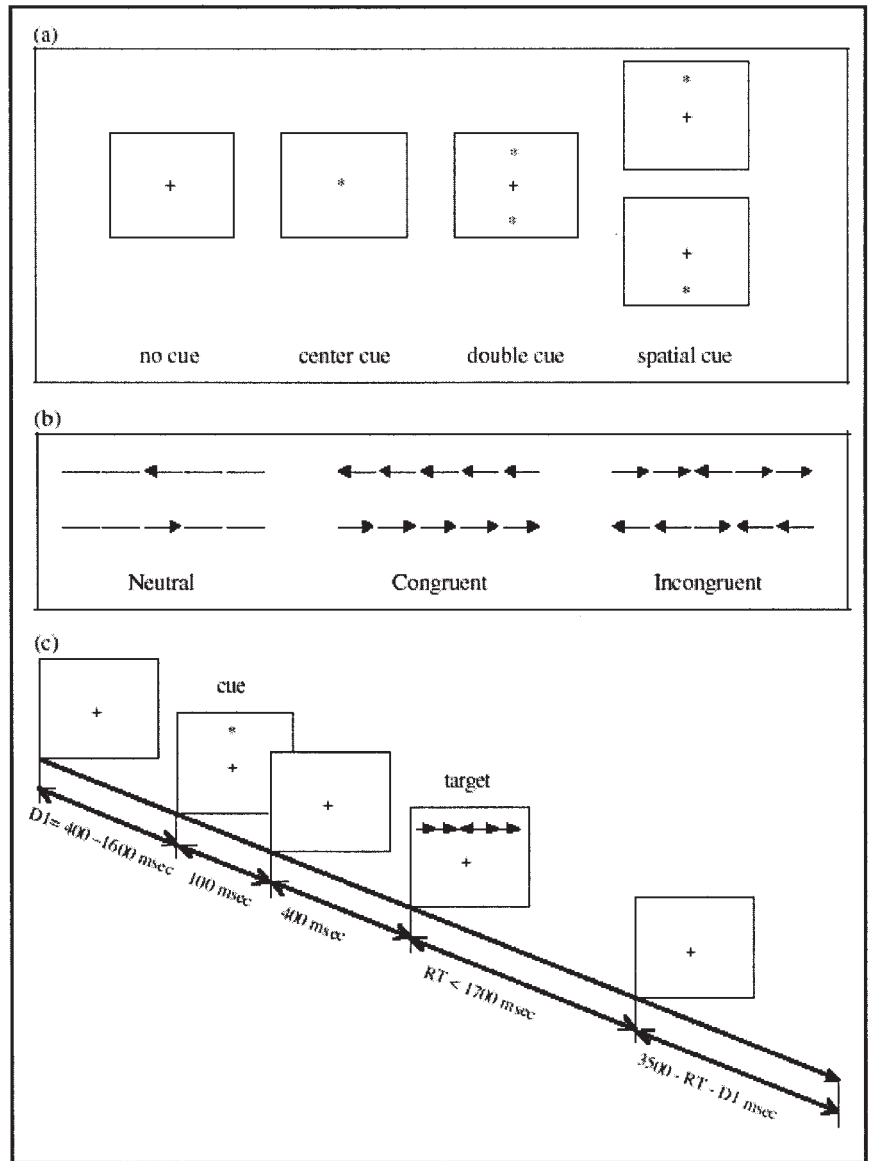
opposite direction. If the fish in question is swimming in the same direction as the surrounding school of fish, the two are congruent; if they face opposite directions, they are incongruent.

Recently, Jin Fan and his colleagues showed that three separate conflict-resolution tasks activate a common conjunction area involving the ACC, together with a conjunction area corresponding to the prefrontal cortex (Fan et al., 2003a). These data highlight the brain network involved in aspects of self-regulation.

It was in this context that the attention network task (ANT) was developed (Fan et al., 2002). The ANT, a variation of the Eriksen Flanker task, requires a subject to determine whether the central arrow points rightward or leftward while the sur-

rounding arrows may be either congruent or incongruent (Box 2 Fig. 2). This design permits researchers to measure the subject's ability to resolve conflict, or cognitive regulation, by subtracting the congruent reaction time from the incongruent reaction time. However, before the task starts, the subject is given a cue, which may be no cue at all, a double cue (alerting the subject to get ready because the target is about to occur), or it may be a cue orienting the subject to the target's location. This design permits two additional subtractions in order to extract both a measure of alerting and a measure of orienting. Analysis of reaction time data reveals little correlation between these three tasks. Although small interactions do occur, such as when the orienting cue occurs at the target location, there appears to be relative independence between the congruency condition and the alerting and orienting conditions. Using fMRI, Jin Fan has also shown activation of unique neuroanatomical sites for each attentional network. The alerting network elicits a strong thalamic activation, while orienting activates superior and inferior areas of the parietal lobe and the conflict or executive network induces activation at the ACC and lateral prefrontal cortex. Whereas many other studies have measured these attentional networks separately, the ANT allows measurement of all attentional networks within one relatively short task that can be run with children and animals, as well as adults and patients.

Box 2. (Continued)



Box 2 Figure 2. Experimental procedure for the ANT. a: The four cue conditions. b: The six stimuli used in the experiment. c: The task as it unfolds in time. Adapted with permission from Fan et al. (2002).

Box 2. TABLE 1. Attentional networks: brain regions and neuromodulators

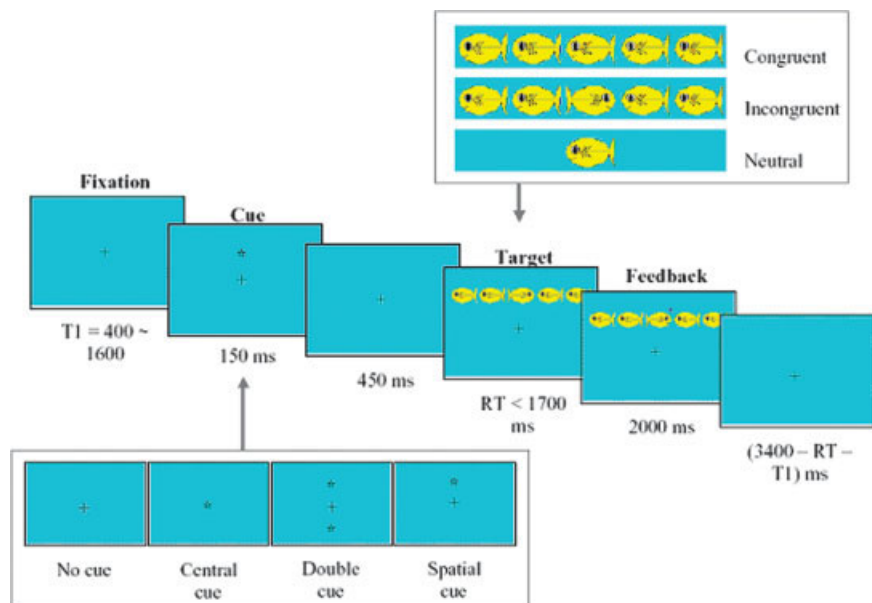
Attentional network	Neuroanatomy	Neuromodulator
Select (executive, conflict, supervisory, focal, metacognitive attention)	Anterior cingulate cortex; lateral ventral prefrontal cortex; basal ganglia	Dopamine
Orient	Superioparietal; temporoparietal; frontal eye fields; superior colliculus	Acetylcholine
Alert (arousal, vigilant attention)	Locus coeruleus; right frontal and parietal cortex	Norepinephrine

Box 3. Development and Training of Attentional Networks

The ANT (see Box 2) has been carefully crafted for use with children by replacing the symbolic flanker arrows with age-appropriate fish stimuli, adding the motivating story of feeding the central fish, and providing brief audiovisual feedback (Box 3 Fig. 1). Behavioral results from two studies in healthy pediatric populations show that the three scores of the fish ANT (FANT) do not correlate and interactions do not exist between them (Rueda et al., 2002). (FANT was coined as a tribute to Jin Fan, who, together with Michael I. Posner and colleagues, developed the ANT and its versions. A combination of “Fan” and “ANT,” the FANT refers to the child ANT.) Whereas there is stable improvement in latencies and errors between 6- and 10-year-old subjects, FANT scores do not show reliable changes at these ages. Direct comparison of children and adults suggests that the alerting and conflict networks, but not the orienting network, continue to improve with age.

The development of attentional networks must involve both genes and specific experience (Fossella et al., 2002a,b; Fan et al., 2003c). The executive attention network as indexed by the ANT shows a strong development from 4 to 7 years of age, but does not seem to change from age 7 to adulthood (Rueda et al., 2002, 2004a,b). During this period, the efficiency of executive control as measured by the ANT also predicts a number of behavioral and questionnaire measures of attentional regulation among normal individuals (Posner and Rothbart, 2000; Rothbart et al., 2004).

Complementing earlier developmental assays (Akhtar and Enns, 1989), one recent study involves a cross-sectional experiment with four age groups ranging from six through nine years of age, along with comparisons of children (age ten) and adult performance on both child and adult versions of the ANT (Rueda et al., 2002, in press). The findings reveal that latency and accuracy improve at each age interval and positive values exist for the average efficiency of each of the networks. Whereas executive attention seems stable after age



Box 3 Figure 1. Sketch of the sequence of (F)ANT trials. Scores are obtained using the following subtractions: select = (RT incongruent) – (RT congruent); orient = (RT central cue) – (RT spatial cue); alert = (RT no cue) – (RT double cue). See BOX 2 for more information. Adapted with permission from Rueda et al. (2004a).

7, alertness can change up to and beyond age 10. Although alerting is steady during middle childhood, efficiency scores for children are much higher than in adults. Perhaps higher alerting scores reflect a child’s difficulty in maintaining the alert state without a cue. Orienting scores, however, do not vary by age in this study; orienting to the correct location produces a similar improvement in reaction time across all ages. Furthermore, ANT data collected from 40 7-year-old children suggest that, as with adults, efficiency scores for the three attentional networks are independent under some conditions. Lack of correlation may also reflect unreliability rather than independence.

Whereas executive attention plateaus after 7 years of development, the orienting network seems to be formed as early as age 4. In more complex situations, where orienting is combined with different dimensions, there may be a later development. The same might be true of many conflict tasks that rely not only on the network that has been discussed but also on other networks such as those involved in planning and other higher-

level functions. The alerting network, however, continues to develop throughout adolescence and into adulthood. Clearly, children’s difficulty maintaining a task set in the absence of a cue telling them to get ready is an important aspect of later childhood and relates to the ability to maintain task sets without specific instructions.

These collective findings indicate the possibility of tracing differences in the development of these networks for children with different genotypes and attentional capacities. Researchers have developed training exercises designed to influence the rate of development of attentional networks (Berger et al., 2000). Using these exercises on children with different genetic and attentional backgrounds presents the opportunity for specific studies of genetic-environmental interaction and individual differences (Fan et al., 2003; Posner, 2004c; Sommer et al., in press).

Understanding how attentional networks function in the everyday life of a child is a key reason for studying the development of these networks. Potential effects on learning and training are of particular conse-

Box 3. (Continued)

quence. Whereas training in non-human animals can persist for hundreds of thousands of trials, assessing the effects of training in human and especially in children can be difficult. Training for only a few days would be unlikely to have a large effect on behavior, but may cause minimal changes that would indicate greater potential benefits of more extensive attentional training. Given this premise, Posner and his colleagues conducted a 5-day attentional training pilot. On the first and last day, they examined the children's EEG during the ANT task, as well as their behavioral data, IQ, and temperament measures. Preliminary analyses indicate that even a brief 5-day attentional training shifts the attentional networks of children toward a more

adult-like pattern. Additionally, the data also show a striking increase in IQ, suggesting the generalization of these effects. Specifically, the experimental group improves significantly in the matrix portion of the child version of the IQ test. Thus, attentional training appears to improve the underlying neural networks involved in conflict resolution and may even generalize to different tasks (Posner, 2004c).

Similar findings have been reported in 8-year-old children diagnosed with ADHD. After completing a training program to strengthen working memory, participants have significantly improved motor performances and IQ results on the nonverbal complex reasoning task of the Raven's progressive matrices (Klingberg et al., 2002, in press; Olesen et al., 2004). These

data suggest that working memory training potentially could be of clinical use for ameliorating the symptoms in ADHD. Training efforts similar to the above-mentioned attentional assays have been reported in adults and children with ADHD (Posner, 2004c). As neuroimaging begins to unravel the effects of practice on brain substrates (Garavan et al., 2004; Landau et al., 2004), cumulative data suggest that these attentional networks can be modified. Introducing attentional training in preschools or childcare centers may be a valuable innovation. Attentional training might be of particular importance because it forms specific neural networks involved in multiple domains of behavior (Posner, 2004c).

ing, error detection, novel or not well-learned responses, difficult or dangerous conditions, and in overcoming habitual actions. The ACC and lateral frontal cortex are target areas of the ventral tegmental dopamine system. Brain imaging data have repeatedly shown that the ACC is an important node in this network. More specifically, neuroimaging studies have shown activation of the dorsal ACC in tasks requiring people to respond either to a prepotent response or to a rather strong conflicting dimension. For example, in the classic Stroop task, experienced readers name the ink color of a displayed word (Stroop, 1935). Subjects are usually slower and less accurate in responding to the ink color of an incompatible color word, such as the word "RED" displayed in blue ink, than in identifying the ink color of a control item (e.g., "LOT" inked in red; Fig. 3). Another such task involves subjects responding to the direction of a central arrow when flanking arrows could either point in the same (congruent) or opposite (incongruent) direction (see Box 2 Fig. 2). The ANT uses this flanker task to measure conflict. Such conflict tasks have been shown by neuroimaging studies to activate the lateral prefrontal cortex, frontal areas such as the

dorsal ACC, and parts of the basal ganglia. These experimental tasks provide a means of fractionating the functional contributions of areas within the executive attention network. Chiefly, the ACC is more active on incongruent than on congruent trials. This difference could reflect the general finding that lateral areas are involved in representing specific information over time, while medial areas are more related to the detection of conflict.

Patients with focal brain lesions of the ACC initially display deficits of voluntary behavior. The notion of ACC involvement in cognitive control and volition has been a topic of much interest lately. Based on behavioral, optical, and neuroimaging data, we recently reported that effective post-hypnotic suggestion, or verbal exhortation, to construe words as meaningless symbols can modulate focal brain activity in highly suggestible individuals (Raz et al., 2002, 2003; Raz, 2004). This top-down influence is both potent and selective: it removes Stroop conflict and reduces neuroimaging signals in both the ACC and extrastriate cortex (Raz, 2004). Whereas a drop in ACC activity is likely related to the abrogation of conflict, the occipital-parietal area may be related to

the visual word-form area, which arranges visual letters into words. Others similarly report that in highly suggestible individuals, hypnotic instructions to view a color image in gray scale prevents normal activation of the color areas of the prestriate cortex (Kosslyn et al., 2000). These data imply that, at least in highly suggestible individuals, attentional manipulations can influence aspects of self-regulation by affecting neural activity in specific brain areas. These findings support the use of special attentional interventions such as hypnosis to study related brain processes (Raz and Shapiro, 2002).

ANT AND LANT

Aspects of laterality and development may operate within attentional networks. For example, human vigilance networks tend to be right-lateralized, while orienting appears to be specific to both modality and hemisphere. PET data collected from healthy individuals show that the right parietal lobe is involved in attentional shifts on either side, whereas the left parietal lobe was involved in attentional shifts on the right side only. Patients with right parietal damage exhibit impaired leftward orienting for both vi-

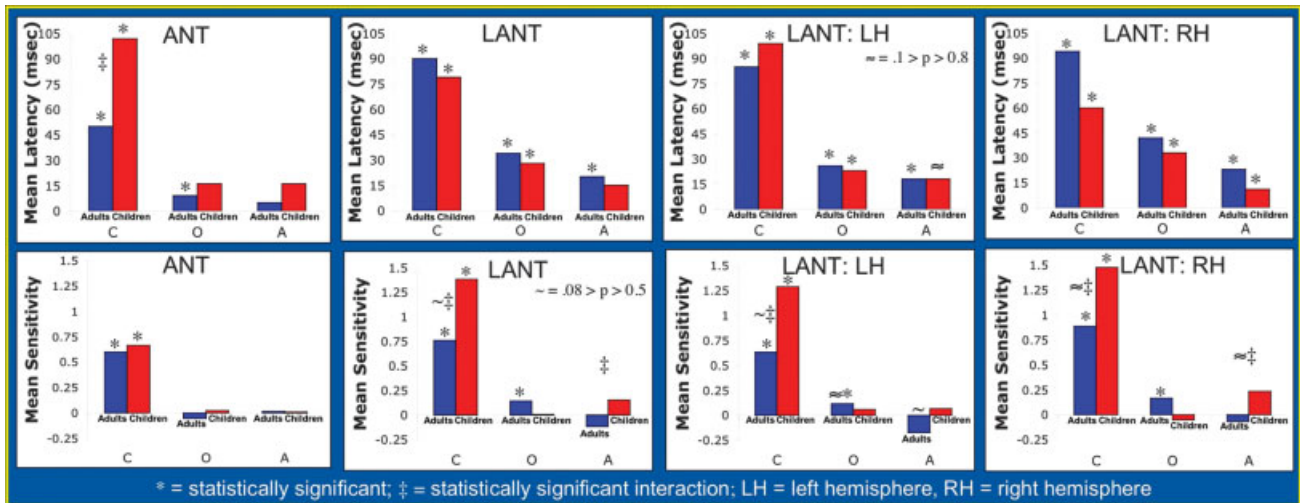


Figure 4. LANT vs. ANT. A lateralized version of the ANT, the LANT assesses the attentional capacity of each hemisphere and has been used to compare hemispheric attentional networks in children and in adults. C, conflict network; O, orienting network; A, alerting network.

sual fields. When the corpus callosum is intact and the two cerebral hemispheres are in normal communication, a single focus of orienting is maintained. However, when the callosal commissures are disconnected, as in split-brain patients, each hemisphere has a partly separate focus for orienting (Zaidel, 1995). From a modality perspective, visual, tactile, and auditory neglect seem to involve different areas of the parietal lobe. Nonetheless, the phenomenon of cross-modal integration, in which visual information influences the location from which we hear sounds, suggests that these areas do communicate.

Eran Zaidel and colleagues recently addressed these issues by using a lateralized ANT (LANT) to examine hemispheric asymmetries associated with the development and performance of attentional networks (Barnea et al., 2004a). A recent study explored the potential effects of neurofeedback, an operant conditioning protocol for self-regulating brain activation patterns by rewarding enhancement or reduction of specific EEG frequencies measured over selected scalp locations. In the study, both ANT and LANT were administered to ten 11-year-old girls both before and after 20 half-hour neurofeedback sessions. Preliminary analysis of the data revealed that neurofeedback improved overall performance. On the ANT, training decreased conflict and increased orienting and alerting, and neurofeedback had specific effects de-

pending on the training side involved. On the LANT, conflict and alerting were unaffected, but neurofeedback enhanced orienting in the left visual field (Barnea et al., 2004b,c, in press c). Overall, the neurofeedback training reduced conflict and increased alerting in the ANT but not in the LANT. Therefore, ANT stimuli likely engage complex interhemispheric interactions as each hemisphere orchestrates different bilateral control circuits.

Another study examined the role of developmental stage on L/ANT performance (Barnea et al., 2004a). Twenty-five young Israeli adults (25–30 years of age) and fourteen Israeli children (10–12 years of age) performed both the ANT and the LANT. The results show that in both adults and children, the LANT generally yields larger, more reliable estimates of the three networks. In adults given the L/ANT, conflict and orienting in the ANT selectively correlate with the LANT in different brain hemispheres: ANT conflict correlates with conflict in the left hemisphere (LH) LANT conflict, and orienting in the ANT correlates with orienting in right hemisphere LANT. Whereas conflict is equal and significant in both hemispheres, the RH specializes in orienting. Compared to adults, children have a larger conflict in both the ANT (latency measures) and the LANT (sensitivity measures). Orienting is significant only for adults within the RH (Fig. 4). Further

research with the LANT will likely further elucidate issues related to attention and laterality.

CONCLUSION

Researchers in the field agree that attention is not a unitary term. Rather, we can fractionate attention into subsystems of more circumscribed function and anatomy. Neuroimaging of the human brain permits us to view attention as an organ system with its own unique anatomy. This attitude facilitates detailed examination of the synaptic, cellular, and genetic basis of normal attentional networks as well as pathological processes. Moreover, we can then link attention to the study of brain states that change both as a function of arousal level (from wakefulness through hypnosis to deep sleep) and across development, from infancy to adulthood. Studies of attention suggest that our subjective experience and cognitive control are associated with these brain networks. The characteristics of these networks and their development in phylogeny and ontogeny thus become central issues of brain research of particular importance to psychology. Pioneered by Michael I. Posner, this approach provides a basis for considering the many pathologies of attention due to insults to the adult brain, developmental disorders, and gene-environment interactions.

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