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Review article

Cognitive Neuroscience of Attention

From brain mechanisms to individual differences in efficiency

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Abstract: Aspects of activation, selection and control have been related to attention from early to more recent theoretical models. In this review paper, we present information about different levels of analysis of all three aspects involved in this central function of cognition. Studies in the field of Cognitive Psychology have provided information about the cognitive operations associated with each function as well as experimental tasks to measure them. Using these methods, neuroimaging studies have revealed the circuitry and chronometry of brain reactions while individuals perform marker tasks, aside from neuromodulators involved in each network. Information on the anatomy and circuitry of attention is key to research approaching the neural mechanisms involved in individual differences in efficiency, and how they relate to maturational and genetic/environmental influences. Also, understanding the neural mechanisms related to attention networks provides a way to examine the impact of interventions designed to improve attention skills. In the last section of the paper, we emphasize the importance of the neuroscience approach in order to connect cognition and behavior to underpinning biological and molecular mechanisms providing a framework that is informative to many central aspects of cognition, such as development, psychopathology and intervention.

Keywords: attention; alerting; orienting; executive attention; neural networks; development; individual differences; plasticity

1. Varieties of Attention

Defining attention is not easy. This is because the concept of attention has to do with a variety of facets of our daily behavior. Aspects of activation, selection and control have been involved in the construct of attention from early to more recent theoretical models [1,2]. On the one hand, attention is the interface between the vast amount of stimulation provided by our complex environment and the more limited set of information of which we are aware. In this sense, attention is a selection mechanism that serves to choose a particular source of stimulation, internal train of thoughts, or a specific course of action for priority processing, and is closely connected to consciousness. On the other hand, attention has been largely linked to the voluntary and effortful control of action, as opposed to well-learned automatic behavior. Very often we do things automatically. For example, we can perform a quite complex motoric act such as running or biking while our attention is focused in a different activity, as for example appreciating the scene or having a conversation with a colleague. Automatic actions do not require attention. However, in certain situations attention is necessary to supervise goal-directed action. These are situations that involve overcoming an automatic course of action and detecting the need to do so. Also, attention is necessary for detecting errors, and controlling behavior in dangerous and novel or unpracticed conditions [3]. Thus, attention mechanisms are also central to the generation of voluntary behavior, which often involves inhibition of automatic responses. Finally, attending also entails an optimal level of activation. Efficiency of attention is greatly affected by conditions in which our level of activation is compromised, such as fatigue or drowsiness. In sum, attention is a multidimensional construct that refers to a state in which we have an optimal level of activation that allows selecting the information we want to prioritize in order to control the course of our actions.

These three broad aspects of attention can in turn be subdivided in subordinate functions or operations (see Box 1). An important subdivision axis is related to whether the particular function is mostly driven by external stimulation or else relies on endogenous processes such as voluntary intentions or expectations. In the scope of selectivity, attention can be oriented to an object or space automatically because of an abrupt change in stimulation occurring there. This happens, for instance, when somebody waves arms to call our attention or a red sail pops-out in the largely homogeneous bluish background of the sea. On the contrary, attention can also be directed to an object because of its relevance to our current goals. If I search for a friend in a crowd of people and I know that she is wearing a green t-shirt, a useful strategy is to prioritize scanning the scene for green objects. These two modes of guiding attention are respectively referred to as exogenous or stimulus-driven (bottom-up) and endogenous or goal-directed (top-down) orienting of attention [4]. Likewise, the alerting state of the individual can be varied endogenously, for example because of a change in motivation (e.g. I am interested in the topic of a talk), or can be varied exogenously because of a sudden change in stimulation (e.g. the sound of an alarm). Very often sustained or tonic attention relies on voluntary processes while phasic preparation is automatic and linked to changes in stimulation.

Control processes, on the other hand, have been conventionally considered voluntary and endogenous by definition [5], although some authors argue that certain processes related to executive control such as conflict adaptation can be carried out automatically [6]. Nonetheless, the operations that are usually linked to cognitive control are conscious detection, inhibition, and conflict processing [5, 7] (see Box 1). Conscious detection is necessary for voluntarily responding to a target.

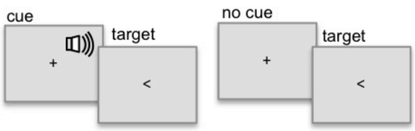
This is easily observed in the context of making mistakes. Errors cannot be corrected unless they are detected. In fact, error detection is very often studied as a cognitive control mechanism involved in action regulation [8]. Another way to study executive control in the lab consists of inducing conflict between responses by instructing people to execute a subdominant response while suppressing a dominant tendency. A basic measure of conflict interference is provided by the well-known Stroop task, although conflict can also be induced by presenting distracting information that suggest an alternative incorrect response, as in the Flanker task (see Box 1). In both types of conflict-inducing tasks, inhibition is necessary to withhold the dominant incorrect response and develop the appropriate one. However, inhibitory mechanisms have been also implicated in the domain of memory representations and perceptual selection, as a way to control attention in these domains [9].

Box 1. Varieties of attention and marker tasks. Different processes have been linked to each function of attention. Several of the most popular marker tasks to measure processes related to activation, selection and executive control are presented below.

Activation

Process: **Preparation**

Tasks: **Warning cues**: Responding to a target that is preceded by a warning cue (compared to when no cue is presented)



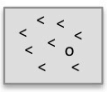
Process: **Sustained attention / Vigilance**

Tasks: **Clock task** (Mackworth, 1948): Responding to infrequent targets, as detecting when double jumps of a clock hand occur

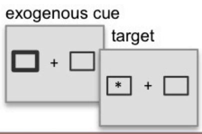
Selection

Process: **Stimulus-driven (bottom-up) orienting**

Tasks: **Pop-out**: Finding a target (o) that doesn't share basic features with distracting stimuli

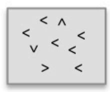


Exogenous orienting cues: Peripheral cues that consist on abrupt changes in stimulation

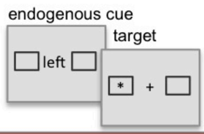


Process: **Goal-directed (top-down) orienting**

Tasks: **Search**: Finding a target (>) that does share one or more basic features with distracting stimuli



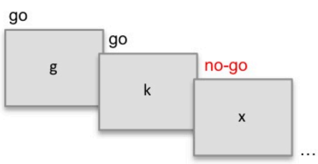
Endogenous orienting cues: Must be interpreted and (voluntarily) followed to orient attention



Control

Process: **Inhibition**

Tasks: **Go-NoGo**: Not responding to a particular stimulus (x) in a context of rapid responses to similar frequent stimuli



Process: **Conflict resolution**

Tasks: **Stroop-like tasks**: Responding to a non-dominant feature of a target (Stroop, 1935)

Flanker task: Responding to a central stimulus surrounded by distracters (Eriksen & Eriksen, 1974)

Most activities of daily life engage all three different aspects of attention. However, differentiating them is relevant because neuroimaging studies in the past have shown that they are associated with brain circuits with relative independent anatomy and neurophysiology. One of these involves changes of state and is called alerting network. The other two are closely involved with selection and are called orienting and executive attention networks [10, 11]. The alerting network deals with the intensive aspect of attention related to how the organism achieves and maintains the alert state. The orienting network deals with selective mechanisms operating on sensory input. Finally, the executive network is involved in the regulation of thoughts, feelings and behavior.

Several years ago, Fan and colleagues developed an experimental task to measure the three attention networks, called the Attention Network Task (ANT) [12]. The ANT is based on traditional experimental paradigms to study the functions of alerting (preparation cues), orienting (orienting cues) and executive control (flanker task) (see Figure 1). Completion of the task allows calculation of three scores related to the efficiency of the attention networks. The alerting score is calculated by subtracting reaction time (RT) to trials with preparation cues from RT to trials with no cue. This provides a measure of the benefit in performance by having a signal that informs about the immediate upcoming of the target and using this information to get ready to respond. The orienting score provides a measure of how much benefit is obtained in responding when information is given about the location of the upcoming target. It is calculated by subtracting RT to targets preceded by cues that inform about the location in which the target is about to appear from that of trials with invalid cues, which trigger attention to an incorrect location. Finally, the executive attention score indicates the amount of interference experienced in performing the task when stimulation conflicting with the target is presented in the display. It is calculated by subtracting RT to congruent trials from RT to incongruent trials. Larger scores indicate more interference from distractors and therefore less efficiency of conflict resolution mechanisms.

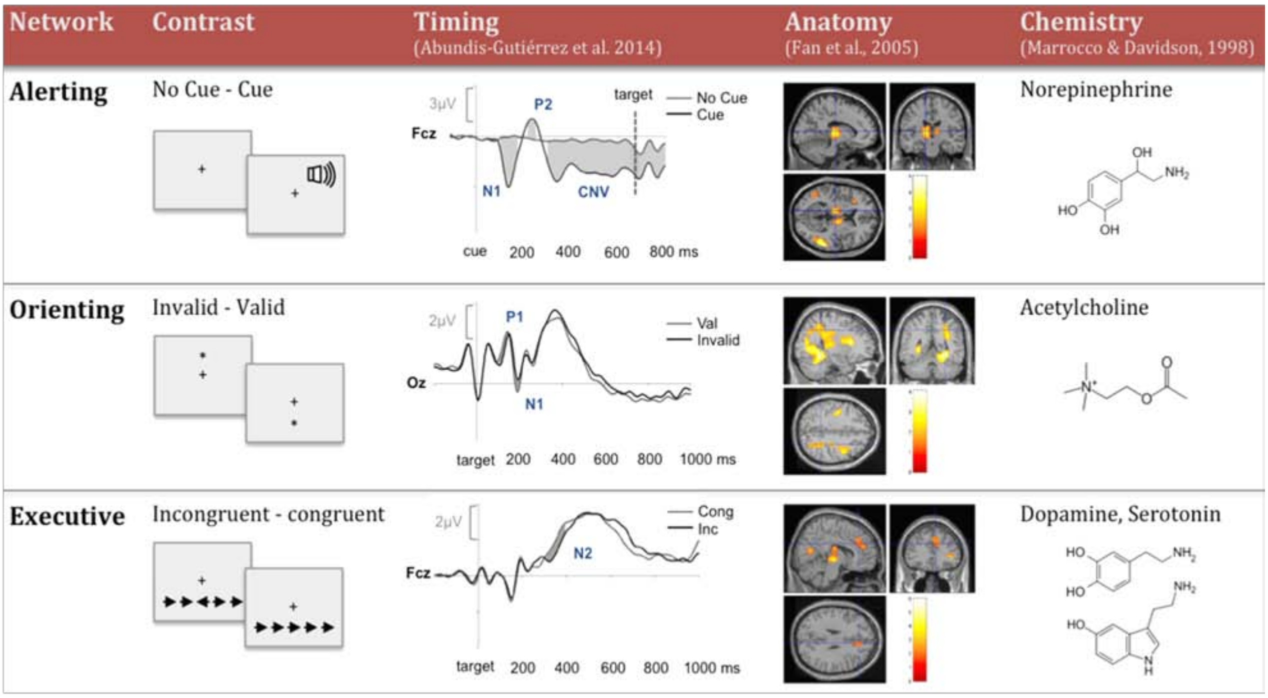


Figure 1. Attention Networks. This figure presents results obtained with different methodologies (from left to right: ERPs, fMRI, and Pharmacological manipulations) using experimental contrasts frequently used to manipulate the engagement of each attention network. The presence of warning cues in contrast to the absence of them (no cue) produces phasic alerting and leads to strong and fast (within half-second after presentation of the cue) neural responses involving a number of brain regions, which can be modulated by altering levels of norepinephrine in the brain. Likewise,

contrasting valid and invalid spatial orienting cues allows studying disengagement and switching attention from one location to another. This engages areas of the parietal and frontal cortices and is facilitated by nicotine, an agonist of the neurotransmitter acetylcholine. Finally, the presence of distracting information that is incongruent (as opposed to congruent) with the response suggested by the target produces conflict and engages executive attention. Conflict is associated with an electrophysiological response occurring as early as 200 ms following the presentation of the stimuli. This response has also been associated with activation of a number of brain regions, including the anterior cingulate and prefrontal cortices, and is modulated by levels of dopamine and serotonin in the brain.

Despite the relative anatomical independence of attention networks, research has revealed that they show some degree of integration and interaction at the functional level. This is expected because, as mentioned earlier, the three attention functions are involved in most attentive activities of our daily behavior. Studies with the ANT task or variations of it have revealed that the networks interact at the functional level [13,14]. For instance, warning signals prompt to rapid automatic responses as opposed to the slower and more carefully weighted decision making processes associated with the executive control system. Thus, the presence of alerting signals leads to faster responses overall but have a detrimental effect on the accuracy of performance, leading to greater interference scores in conflict tasks. This can be due to the acceleration of response selection processes [15] or to a broadening of the spatial scope of attention [16] following the presence of warning cues. On the contrary, valid orienting signals facilitate focusing of attention on relevant targets and hence the suppression of irrelevant distracting information, resulting in lower interference scores (i.e. more efficient executive control of attention). Finally, warning signals also appear to accelerate orientation of attention, particularly when alerting and orienting cues occur close in time [13]. These functional interactions have also been characterized in children in the same direction as adults, with the particularity of the alerting x executive interaction, which moves from a facilitatory effect of alerting cues over executive attention early in childhood to the adult pattern of interaction by 12 years of age [17].

2. Neural Mechanisms

Using the ANT task with brain imaging or electrophysiological techniques we can study the neuroanatomy of attention functions and the timing of activation of each brain network. Also, pharmacological studies have provided substantial information about the neurochemical modulators of each function. The information provided by many studies using the ANT, or parts of it, is summarized in Figure 1. As can be observed in this figure, the activation associated with marker tasks of each attention function is not restrained to a single brain structure; instead a number of rather distant brain regions are activated by experimental contrasts measuring each attention process. Also, regions involved in particular functions have shown significant patterns of functional correlations at rest, at least in the case of orienting [18] and executive attention [19], as will be discussed in the next sections. For this reason, the term “brain network” is used to describe the neural basis of attention functions in the Posner’s model of attention [10,20].

2.1. Alerting network

Arousal of the central nervous system involves input from brain stem systems that modulate activation of the cortex. Primary among these is the locus coeruleus (LC), which is the source of the brain's norepinephrine (NE). We know that drugs that block NE prevent the changes in the alert state that lead to improved performance after a warning signal is provided [21]. It has been demonstrated that the influence of warning signals operates via this LC-NE system, which exhibits phasic and tonic modes of activity [22]. In the phasic mode, the system react to warning signals in a short timescale by facilitating decision processes that optimize performance in a particular task. In the tonic mode of activation, the system optimizes performance across tasks promoting a more exploratory mode of alertness. To monitor for task-related utility, the LC is prominently connected to the anterior cingulate and orbitofrontal cortices, structures that are involved in representing action-goals and intentions.

Studies involving patients with lesions of the frontal and parietal lobe, particularly in the right hemisphere, as well as imaging studies with healthy people have shown the involvement of these regions in the endogenous maintenance of the alert state in absence of warning signals [23]. However, the neural basis for endogenous activation may differ from those involving phasic changes of alertness following warning cues. Warning signals provide a phasic change in level of alertness over milliseconds intervals. Event-related potentials (ERPs) provide precise information about the time in which the brain responds differently to presence/absence of alerting cues. The presence of alerting cues produces dramatic changes in brain activation from early on, followed by a sustained negative ERP component called the contingent negative variation (CNV). Several studies have shown that the CNV is generated by activation in the frontal lobe, with specific regions depending on the type of task being used [24]. When using fixed cue-target intervals, warning signals are informative of when a target will occur, thus producing a preparation in the time domain. Under these conditions, warning cues appear to activate fronto-parietal structures on the left hemisphere, instead of the right [25].

2.2. Orienting network

Orienting attention is an important mechanism for conscious perception. The attention system achieves selection by modulating the functioning of sensory systems. Attended stimuli generate early event-related potentials (ERP) of larger amplitude than unattended ones (see Figure 1), suggesting that attention facilitates perceptual processing of attended information from very early stages of processing [26,27]. Attention is thus considered a mechanism that allows selecting out irrelevant information and gives priority to relevant information for conscious processing. Studies using fMRI and cellular recording have demonstrated that brain areas that are activated by attention cues, such as the superior parietal lobe and temporal parietal junction, play a key role in modulating activity within primary and extrastriate visual systems when attentional orienting occurs [4,28].

Studies that combine neuroimaging techniques with orienting paradigms such as those depicted in Box 1, have led to the identification of two different brain networks involved in selective attention. The two networks are distinctively activated 1) when focusing attention voluntarily using top-down control mechanisms, or 2) when exogenous and relevant stimuli appear in the environment inducing reorienting of attention according to task demands. In the first case, performance of top-down orienting tasks has been associated with the activation of a bilateral dorsal-frontoparietal network that involves the intra-parietal sulcus (IPS), the superior parietal lobule (SPL) and the frontal eye fields (FEF). In the second case, detection of infrequent or miscued targets has been related to increased activation in a right-lateralized network of ventral fronto-parietal structures including the temporo-parietal junction (TPJ) and inferior frontal cortex [4,29].

During the last decades, a great amount of research has characterized the structural and functional features of these two attention systems. Perhaps one of the most compelling findings in the field is that activation of the dorsal and ventral attention systems is not limited to the performance of a task, the presentation of stimuli or the engagement of attention resources [30–32]. In fact, analyses of spontaneous BOLD fluctuations at rest have revealed that the two attention systems are clearly segregated and exhibit only a small overlapping region in the prefrontal cortex [18]. Recent studies on the white matter structural connectivity of the two networks have further supported this anatomical separation [33]. At the functional level, temporal differences in the neural activation of the two networks have also been reported. Electrode recordings in monkeys have demonstrated that activation of structures within the dorsal network reaches significance levels before ventral structures when monkeys perform a visual search task (endogenous orienting), whereas activation of structures in the right-lateralized ventral network reaches significance levels earlier under pop-out (exogenous orienting) conditions [34].

Despite their anatomical and functional dissociation, the dorsal and ventral systems dynamically interact to ensure a flexible and efficient control of attention [35]. As a matter of fact, damage in ventral regions affects inter-hemispheric physiological activity between unaffected regions of the dorsal system, particularly the IPS [36]. Moreover, when a person is engaged in a task, structures in the dorsal system sends top-down signals that not only modulate sensory systems according with current goals [37], but also suppress the activation of the ventral system to restrict its activation to stimuli that are relevant [29]. Thus, when salient cues carrying out relevant information for the task are presented, the right TPJ exhibits a significant increase of activation that is associated with improved performance of the task [38].

2.3. Executive attention network

We know from numerous neuroimaging studies that diverse conflict tasks show a common node of activation in the anterior cingulate cortex (ACC) [39]. In a meta-analysis of imaging studies, the dorsal section of the ACC was activated in response to Stroop-like conflict tasks, whereas the ventral section appeared to be mostly activated by emotional tasks and emotional states [40]. The two divisions of the ACC seem to interact in a mutually exclusive way. For instance, when the cognitive division is activated, the affective division tends to be deactivated and vice-versa, suggesting the possibility of reciprocal effortful and emotional controls of attention [41]. Also, resolving conflict from incongruent stimulation in the flanker task activates the dorsal portion of the ACC together with other regions of the lateral prefrontal cortex [39,42]. The conflict monitoring account proposed by Botvinick and colleagues [43] suggest that the ACC is involved in conflict detection and monitoring, while lateral frontal areas are in charge of solving the conflict. This account is congruent with the finding that performing different conflict tasks activates distinctive structures of the prefrontal cortex, but shows a common burst of activation in the ACC [39].

Studies using electroencephalography also inform about the temporal dynamics of conflict processing. The presence of conflict modulates the N2 potential, a negative midline fronto-parietal component that peaks around 200–400 ms after the presentation of the target stimulus [44]. N2 amplitude increases in incongruent trials relative to congruent ones signal greater effort to suppress the processing of dominant but incorrect dimension of the target (see Figure 1). This effect has been related to control processes arising in the ACC [45].

The structure of connections of the ACC with other brain regions makes it a good candidate for executive control. Different parts of the ACC are well connected to a variety of other brain regions, including limbic structures as well as parietal and frontal areas [46]. Recent studies have examined the connectivity of the executive network at rest and have shown that two functionally different but complementary circuits are engaged when implementing cognitive control: the fronto-parietal and the cingulo-opercular networks [19]. The fronto-parietal network is related to processing of cognitive control signals that potentially initiate response adjustments on a trial-by-trial basis. This network includes the dorsolateral prefrontal cortex (dlPFC), inferior parietal lobule (IPL), dorsal frontal cortex (dFC), intra-parietal sulcus (IPS), precuneous, and middle cingulate cortex (mCC). On the other hand, the cingulo-opercular network is involved in maintaining a stable task set during performance; that is, representing the goal of the individual in the context of the task and the corresponding stimulus-to-response mapping along many trials. This network includes the anterior prefrontal cortex (aPFC), anterior insula/frontal operculum (aI/fO), dorsal anterior cingulate cortex/medial superior frontal cortex (dACC/msFC) and the thalamus [47].

The conflict monitoring and dual network models of executive control have similarities in terms of which anatomical structures are engaged in control processes, however they propose different functional dynamics of the control system. The conflict monitoring account favors a single unified executive system in which the lateral prefrontal cortex provides top-down control signals guided by monitoring signals generated by midline structures. On the other hand, the dual network view proposes an independent functional dynamic of these two systems by dividing processes that entails stable background maintenance for task performance (cingulo-opercular circuit) from processes related to the online response adjustments in a trial-by-trial basis (fronto-parietal circuit). Although both models explain considerable amount of data, it has been suggested that the dual network model presents a more suitable account of the executive attention network, particularly when studies from lesions in humans and animals as well as studies related to the directionality of relationships between control processes are taken into account [10].

3. Efficiency of Attention

People differ greatly in their attention skills. The degree of competency can be measured at the cognitive level with the type of tasks described in the previous sections (as well as in Box 1 and Figures 1 and 2). With the range of neuroimaging methods currently available, levels of competency can be associated with patterns of brain activation as well as other neurophysiological and structural aspects of the brain. The level of competency or efficiency of attention mechanisms is subject to variation due to multiple factors. One important source of variation is the maturation state of the individual. Tremendous gains in efficiency occur over development, particularly during the first years of life. However, maturation of the attention system is also influenced by biological factors of genetic origin as well as experiential aspects related to family/social environment and education. We briefly review these different sources of attentional variation in the next sections.

3.1. Development of attention

Each of the functions of attention considered in the neurocognitive model described above is present to some degree in infancy, but each undergoes a long developmental process [48]. Both reactive and self-regulatory systems of attention are at play during the first years of life. Initially, reactive attention is involved in more automatic engagement and orienting processes. By the 12th post-natal week the infant has become able to maintain the alert state during much of the daytime hours, although this ability still depends heavily upon external sensory stimulation, much of it provided by the caregiver. Then, by the end of the first year of life, attention can be more voluntarily controlled. Across the toddler and preschool years, the executive system increasingly assumes control of attention processes, allowing for a more flexible and goal-oriented control of attention resources.

At about 3 years of age, children become more able to follow instructions and perform reaction time tasks. To study the development of attention functions across childhood, a child-friendly version of the ANT was developed [49] (see Figure 2a). This version is structurally similar to the adult ANT but uses fish instead of arrows as target stimuli. This allows contextualization of the task in a game in which the goal is to feed the middle fish (target), or simply making it happy, by pressing a key corresponding to the target direction. Using the child ANT, changes in efficiency with age for each attention network has been traced during the primary school period into early adolescence. Figure 2b presents networks scores calculated with accuracy data for children between 6 and 12 years of age. Data reveal separate developmental trajectories for each attention network. While alerting shows an earlier maturation course, the orienting and executive networks display a more protracted developmental trajectory during childhood [17]. In addition, performing the child ANT while brain responses are registered informs of neural mechanisms underlying the development of attention networks. Abundis-Gutierrez y colleagues [50] conducted such study using EEG/ERP recordings with children aged 4 to 13 years. Overall, age-related changes were mostly observed on early ERP components, suggesting that, compared to adults, children exhibit a poorer fast processing of conditions varying in attentional requirements. Young children showed poorer early processing of warning cues compared to 10–13 year-olds and adults. Also, children below age 9 years exhibited a poorer processing of orienting cues in early (N1) as well as late (P3) ERP components, indicating that they are not yet able to obtain a full facilitatory effect from valid cues, and must activate the orienting network to a greater extent in order to shift attention when invalid cues are presented. Finally, children showed a delayed conflict-related modulation of frontal components, compared to the N2 modulation observed in adults, suggesting that the executive attention network is not yet fully mature in late childhood.

Age-related gains in behavioral and electrophysiological efficiency are most likely related to changes in structural and functional connectivity observed with neuroimaging techniques. There is evidence that increased attentional performance is associated with greater efficiency of information transfer in the brain, which is characterized by the involvement of distributed (as opposed to clustered and locally-organized) brain nodes and shorter length of paths connecting such nodes [51]. During the first year of life the anterior cingulate shows little or no connectivity to other areas. However, after the first year, infants begin the slow process of developing the long range connectivity that is typical of adults [52]. Moreover, functional connectivity of brain regions involved in attention changes greatly during childhood. While adults show separate functional networks related to orienting and executive attention, these two networks are more integrated in children [53]. In addition, below age 9 children show many short (local) connections instead of the long distance connections involving frontal and parietal regions exhibited by adults [54].

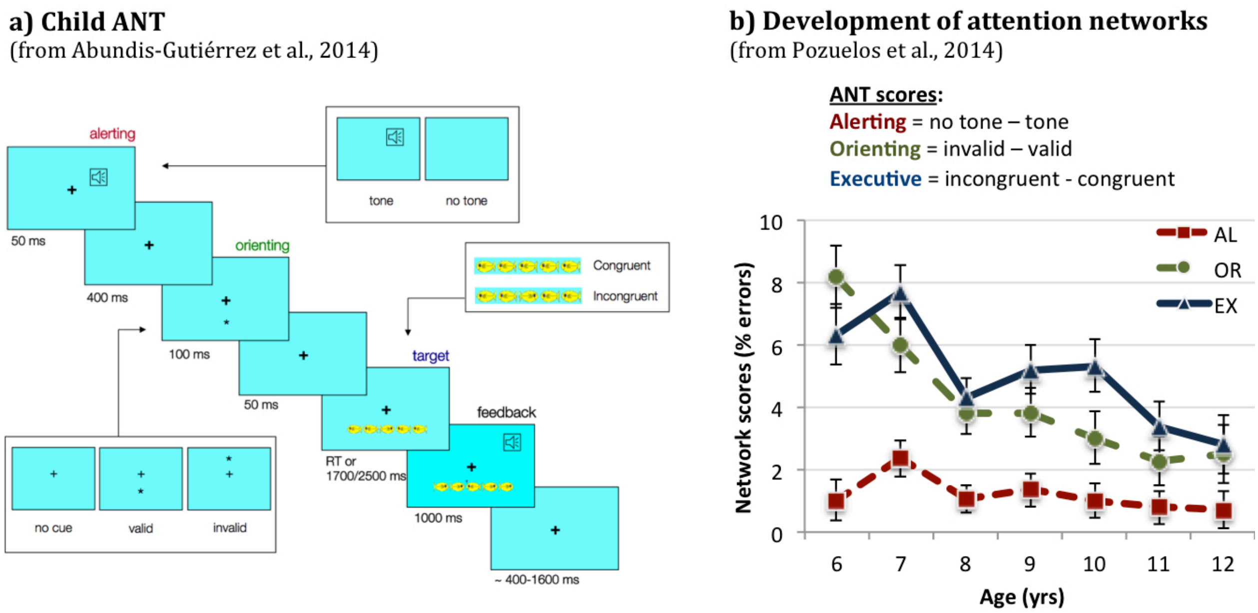


Figure 2. Development of attention networks. (a) Schematic representation of the child ANT. (b) Developmental trajectory of attention network scores (calculated with percentage of errors) between 6 and 12 years of age. Figures reproduced with permission.

3.2. Individual differences

Over and above development, people show differences in attention skills.

In previous sections we have reviewed the structural and functional properties of attention networks. Higher functional efficiency of these networks is associated with a large arrange of skills that are central to our adaptation in the world. But, what makes the brain of an individual more efficient?

3.2.1. Genetic factors

One possible answer to this question is that neural efficiency is determined by the genetic endowment that is inherited from parents. Heritability of the attention networks was tested in a twin study conducted with the ANT. In this study, executive attention and alerting scores showed stronger concordance for monozygotic compared to dizygotic twins, indicating a significant level of heritability for those attention functions, whereas no evidence of heritability was found for the orienting network [55].

Establishing candidate genes for each attention function is facilitated by knowing the neuromodulators related to each network (see Figure 1) [56]. A good number of studies have examined the relation between dopamine-related genes and the executive attention network. Polymorphic variations in genes such as the DAT1, DRD4 or COMT, known to influence efficiency of the dopaminergic system within the prefrontal cortex, appear to explain at least partially inter-individual variability at the level of behavioral [57–59] and brain function [60–62]. Likewise, several studies have examined the association between variations of cholinergic-related genes, such as the CHRNA4 gene, which encodes the neural nicotinic acetylcholine receptor, and the performance of selective attention tasks [63,64]. However, recent evidence shows that dopaminergic markers on DAT1 and COMT genes may also explain inter-individual variability in the performance of orienting attention tasks [65,66]. Furthermore, dopamine and cholinergic genetic markers have also been related to individual differences at the level of temperamental traits related to executive control and self-regulation [67,68].

3.2.2. Environmental and educational factors

Complementary to the influence of genetic factors, much evidence has been provided in recent years in favor on the susceptibility of the neural attention systems to the influence of experience. One piece of evidence comes from studies showing vulnerability of cognitive skills, including attention, to environmental aspects such as parenting and socioeconomic status [69].

Aspects of parent-child relationships have been shown to play a role in the development of attention, especially during the first years of life. The development of self-regulatory skills is promoted by parenting strategies that support children's autonomy [i.e. offering children age-appropriate problem-solving strategies and providing opportunities to use them) [70], whereas strategies of control and intrusiveness appear to be detrimental [71]. Moreover, when dealing with temperamentally challenging children, who are more likely to display externalizing behavior problems, the use of gentle discipline (i.e., give commands and prohibitive statements in a positive tone) results in the development of greater regulatory skills [72]. Results are similar for teacher-child relationships. Supportive teaching appears to safeguard the risk of academic failure in children with poorer regulatory skills [73].

There is also evidence about the impact of the socioeconomic status (SES) of the family in a variety of cognitive functions of the child [74]. It is well documented that children from low-income families show poorer behavioral regulation than children from high SES families [75]. In the attention domain, it has been shown that children who are raised in families with higher SES have more efficient alerting and executive scores in the child ANT [76]. Unfortunately, the impact of SES on children's executive skills is observed already from early infancy. In a recent study, Clearfield & Niman [77] found that during the second half of the first year of life infants coming from low SES families already show delayed development of cognitive flexibility skills compared to infants from high SES families. Data of this sort suggest that functions of the frontal lobe are vulnerable environmental factors. In fact, a recent MRI study carried out with a large number of children shows that parental education significantly predicts cortical thickness in the ACC as well as the left superior frontal gyrus after controlling for a number of other variables such as total brain volume, age, and IQ [78].

It is important to note that the impact of environmental experience in brain structure and function does not imply that SES differences are unchangeable. Rather, this type of data speaks of the plastic nature of the brain, and it is the duty of cognitive neuroscientists to understand and promote the types of experiences that produce the most beneficial outcomes in terms of cognitive and brain efficiency.

4. **Network Plasticity**

In the last decade, there has been growing interest in studying the beneficial influences produced by training programs aiming at improving cognitive performance and brain plasticity. Cognitive training consists in voluntarily engaging in the practice of exercises specifically designed to increase experience in a particular function [79]. It has been suggested that the nature of training exercises may produce either a specific impact on the efficiency of the targeted brain network or a more general influence affecting the dynamical state of the brain [80].

Training programs often consist of computerized exercises that engage the skills they aim to train in increased levels of difficulty. Several studies using these so-called process-based training interventions have shown efficacy gains in attention [58], task switching [81], working memory [82], and inhibitory control processes [83] following training. In order to understand how post-training improvements are related to training-induced brain plasticity, several training studies have been conducted in combination with neuroimaging techniques. Reported findings show that cognitive training influences brain plasticity at different levels. Using EEG, Rueda and colleagues [58] studied training-induced changes in the efficiency of the executive attention networks in a sample of preschool-age children. Their results revealed that attention training produces a reduction of latency and a shift of topography of the N2 component, suggesting a more mature pattern of activation after training (see Figure 3). On the other hand, an increased activation of pre-frontal (middle frontal gyrus) and parietal (intra-parietal, and inferior parietal) regions was reported after working memory training [84]. Also, Jolles and colleagues [85] have shown that fifteen sessions of training with a working memory program result in increased functional connectivity at rest within the fronto-parietal network. Moreover, it has been reported that training induces changes in the binding potential of dopamine D1 receptors in the parietal and prefrontal cortices [86]. Thus, interventions aimed at increasing experience with particular cognitive processes produces changes in a variety of neural mechanisms, which very likely underlie gains in competency observed at the behavioral and cognitive levels.

On a different approach to training, interventions involving group of contemplative practices such as meditation have been shown to produce brain state changes by influencing the operations of different brain networks [80,87]. Meditation is a form of mental training that requires the voluntary engagement of executive functions in order to achieve a non-judgmental attention to present-moment experiences [88]. Several studies have showed that meditation training and expertise result in improvements in behavioral performance of tasks that induce conflict monitoring [89,90], allocation of attentional resources [91] increased activation of the ACC [92] and plasticity of white matter [93]. In this last respect, it has been reported that meditation training produces more efficient connectivity between brain structures [93,94]. In a series of studies, Tang and colleagues explored the impact of meditation training in white matter integrity using Diffusion Tensor Image (DTI). This method allows indexing the integrity of white matter fibers, changes in the morphology of the axons and myelination. Results from these studies suggest that meditation training influences the state of brain dynamics by increasing the number and myelination of white matter fibers [93,95]. According to Posner and colleagues [94], white matter changes may be the underlying mechanism that promotes the improvement of communication efficiency between the ACC and other brain areas, contributing to a change in the state of brain activity.

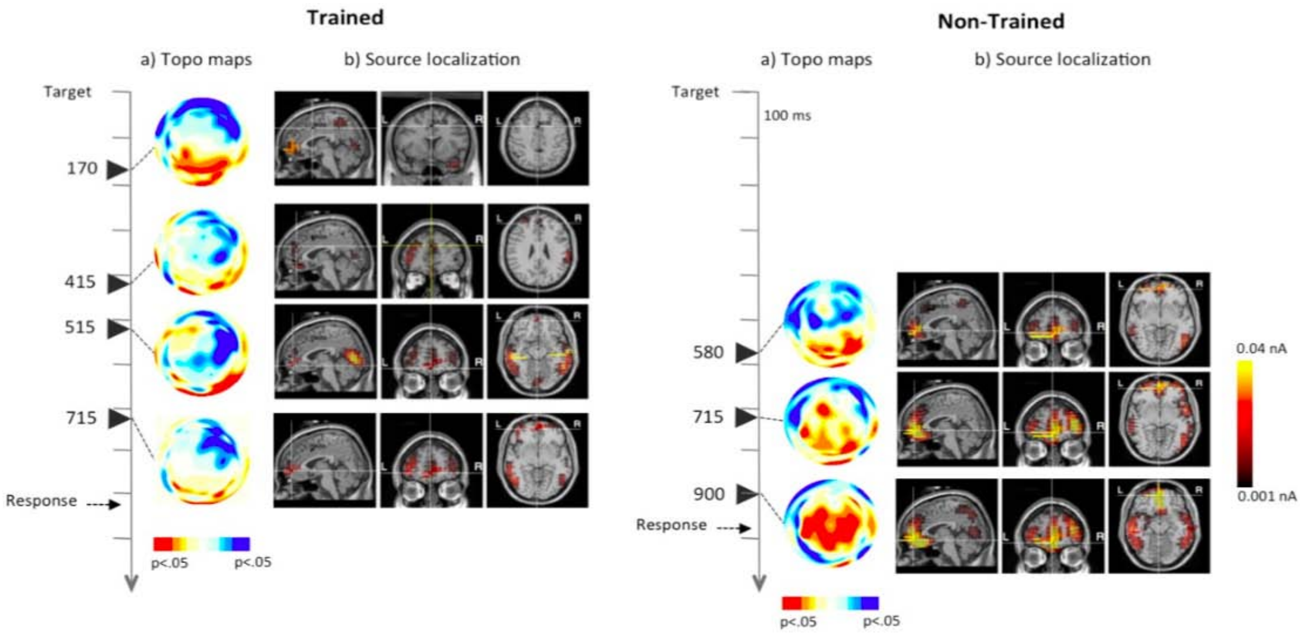


Figure 3. Changes in the timing of activation of the executive attention network following cognitive training in young children. The figure depicts the brain response associated with performance of a child-friendly flanker task (described in Figure 2) measured with ERPs in groups of trained and untrained 5 years-old children. Topographic maps (a) show observed significant amplitude differences between congruent and incongruent conditions from target presentation to response (in 100 ms time intervals), which are associated with particular sources of activation (b) Following eight 45-minutes intervention sessions, trained children exhibited faster neural responses associated with regions within the executive attention network compared to non-trained peers (Reproduced with permission from Rueda et al., 2012).

Cognitive training studies have been important to assess and understand how much we can impact the efficiency of brain networks with theoretically grounded interventions. Data have been reported that show the potential of modifying brain systems in order to improve self-regulatory processes. Although more studies are needed to replicate and validate these findings, evidence to date has shed light into the beneficial impact of training intervention in different processes that promotes mental capital.

5. Summary and Integration

Attention is a superior cognitive function involved in most of our daily life activities. Mostly from the second half of the XXth century on, research in the field of Cognitive Psychology has provided precise experimental methods to measure the different processes involved in this multidimensional construct. Aspects of alertness, orienting and executive control have been differentiated at the cognitive and neural levels. The study of the neural mechanisms of attention has greatly benefited from the impressive technological developments that happened in the last decades, which allow the examination of a wide range of brain processes in living individuals. In this paper, we have reviewed information available on the particular brain circuitry associated with each attention function, as well as neurochemicals modulating each network. Information on the neural mechanisms is central to an understanding of individual differences in attentional efficiency. An important source of variation in efficiency is the level of maturation of the system. Developmental studies provide valuable information on the cognitive and neural changes that occur with age. In turn, this information informs of possible mechanisms underlying differences in competence across individuals over and above age, which can be related to genetic as well as environmental factors. Finally, in recent years, an increasing bulk of studies have examined the impact of cognitive training programs of different nature in behavioral and neural measures, providing compelling evidence on the plastic nature of the brain. Although much research is needed before we fully understand processes of cognitive and brain plasticity following intervention, undoubtedly this research will inform professionals in the fields of Psychology and Education about the best possible strategies to promote people's mental skills.

In this review, we have examined many different aspects related to attention mechanisms, including cognitive, physiological, developmental, genetic, social, and intervention. Each of these areas is involved as we try to understand attention, and an integral model of this central cognitive aspect of human behavior is useful for all these areas of research.

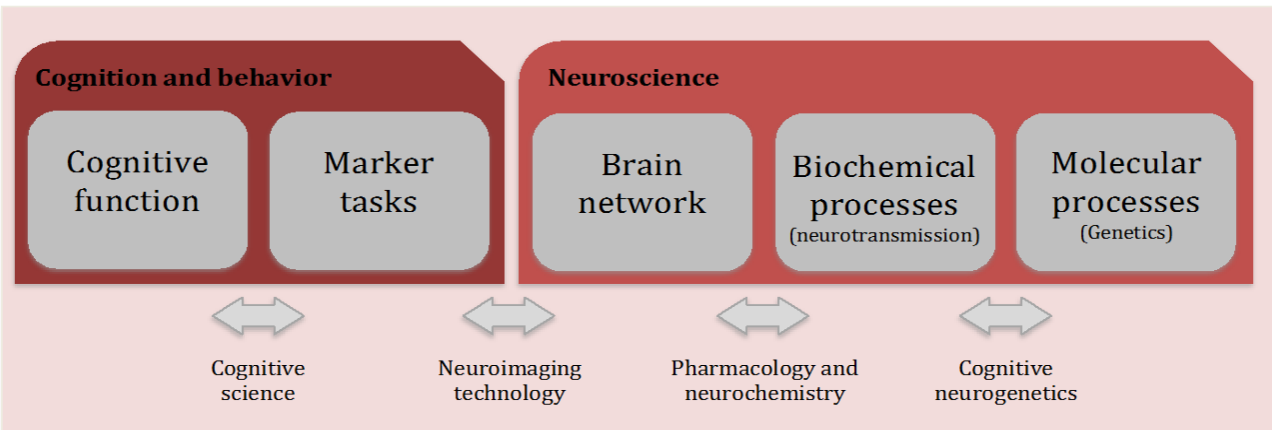


Figure 4. **Path connecting mind to brain.** This figure depicts the different levels of analysis (in gray boxes) and disciplines (presented below the arrows linking the gray boxes) involved in connecting mind and behavior to underlying brain mechanisms.

The path connecting social and molecular aspects of cognition and behavior is a very long one. We hope to have made a good exposition of the idea that this path can only be travelled if we have a good understanding of the neural networks involved in the function we want to explain. The network approach, as first introduced by Hebb in 1949 [96] and nowadays resumed by Posner & Rothbart [20], is vertebral to the many steps to be traveled. Much information is needed to connect a particular cognitive function to the molecular processes that influence it, and the effort to provide this information involves many disciplines (see Figure 4). The extraordinary technological development that has taken place in the last decades allows a much deeper understanding of the mind-brain relationship. Combined with grounded theoretical accounts of cognition, brain-imaging methods are being applied to studies of the circuitry, plasticity and development of neural networks underlying cognitive skills. Together with pharmacological and genetic methods they will be able to provide integral models of mental processes. Due to the convergence of data from multiple levels of analysis, integral models are more likely to reflect the realm of mental phenomena. Further, unified models of cognition partake increased heuristic power. For instance, the integral model of attention presented in this paper is likely to inform of possible pathophysiological mechanisms of developmental diseases involving attention. In turn, the development of efficient interventions to promote attention will be greatly facilitated by knowing the biological factors underlying pathological mechanisms as well as the environmental experiences that promote or prevent them.

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Conflict of Interest

The author declares no conflicts of interest in this paper.

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