Typologies of attentional networks

Amir Raz and Jason Buhle‡*

Abstract | Attention is a central theme in cognitive science — it exemplifies the links between the brain and behaviour, and binds psychology to the techniques of neuroscience. A visionary model suggested by Michael Posner described attention as a set of independent control networks. This challenged the previously held view of attention as a uniform concept. The idea that disparate attentional networks correlate with discrete neural circuitry and can be influenced by focal brain injuries, mental state and specific drugs has since been supported by converging data from several modern methodologies. Given the recent explosion in empirical data, attentional typologies provide powerful conceptual tools with which to contextualize and integrate these findings.

Hypnosis
Attentive receptive concentration that allows certain individuals to change the way they experience themselves and the environment. These individuals often show heightened compliance with suggestion.

Cognitive psychology
The psychological study of the thinking, feeling or acting mind, which cuts across diverse fields of behaviour.

Cognitive neuroscience
The study of how the brain enables the mind.

**MRI Unit, Department of Psychiatry, Division of Child and Adolescent Psychiatry, Columbia University College of Physicians and Surgeons and New York State Psychiatric Institute, 1051 Riverside Drive, P.O. Box 74, New York, New York 10032, USA. ‡Sackler Institute for Developmental Psychobiology, Weill Medical College, Cornell University, 1300 York Avenue, P.O. Box 140, New York, New York 10021, USA.*
Correspondence to: A.R. e-mail: DrAmirRaz@gmail.com

doi:10.1038/nrn1903

Central to many behavioural functions, attention is one of the oldest and most pivotal issues in psychological science[1] (TIMELINE). It refers to both the preparedness for and selection of certain aspects of our physical environment (for example, objects) or some ideas in our mind that are stored in memory. With more research tools becoming available, our understanding of attention is likely to yield innovations in education[2], the treatment of pathological conditions[3], rehabilitation[4] and cognitive training[5] (BOX 1). Improved understanding could also provide insights into cultural and individual differences[6], and further integrate psychological and brain sciences[7]. Most research has been conducted with normal or pathological participants in the context of typical, waking attention, but carefully designed experimentation with states of atypical attention, such as those induced by drug ingestion, meditation and hypnosis, could accelerate this process[8]. In this age of information explosion, conceptual tools are as important as technological ones. Adopting a 'big-picture' approach that encompasses a clear formulation of different typologies and nomenclatures probably would enable better management of experimental findings, which would, in turn, lead to a more focused and cohesive research agenda in the quest to elucidate human attention.

Great minds have grappled with the study of attention, but, in 1890, William James was probably the first to write about its multiplicity[9]. Several researchers have since suggested that there are multiple components to attention (for example, Allan Mirsky and colleagues[10]), and the field of attention is now one of the most studied in the cognitive sciences (FIG. 1). However, at the beginning of the twentieth century behavioural psychology largely postponed research into the internal workings of attention and only resumed this quest during and after World War II, with such luminaries as Kenneth Craik, Norman Mackworth, Colin Cherry and Donald Broadbent[11].

Broadbent viewed attention as a filter, and this model enabled objective studies into the limitations of human ability when dealing with more than one signal at a time in various practical tasks. Thereafter, cognitive psychology elucidated the processes of selection by examining a wide range of everyday phenomena, making them amenable to the controlled conditions of scientific scrutiny. With time, it became increasingly evident that attention can be contextualized as both a form of 'alertness' and as an index to resource allocation. Consequently, attention has been identified less with Broadbent's earlier idea of a filter or bottleneck and more as a mechanism for providing priority for motor acts, consciousness and certain types of memory.

Cognitive neuroscience has posed many questions about attention. For example, does attention select items by enhancing relevant representations or by inhibiting irrelevant ones? And how is attention controlled? Although none of these queries has been fully answered, there is a consensus in several areas (for example, the idea of capacity limitation, the importance of location for selection, as well as the role of the parietal cortex)[12]. More recently, attention has been linked to both emotional regulation and self-regulation[13,14], and effortful control[15,16] and inhibitory control[17]. These themes are being vigorously explored using various research methods under both healthy and pathological conditions, with animals and humans (both young and old), being tested[18].

Unpractised tasks typically demonstrate the limits of attention, but with extensive practise most attention-demanding tasks can become automated or independent

Timeline | **A sketch of selected landmarks in the study of attention**

Year	Landmark
1868	The substration method — one of the most popular methods in cognitive science — is used to study attention by Franciscus Donders.
1891	William James, the American father of modern psychology, mentions 'varieties of attention'.
1921	Behaviourism, together with positivism, is partly responsible for the stagnation in the field of attention research between the 1920s and the 1950s.
1924	Electroencephalography is introduced to eavesdrop on the brain's spontaneous electrical activity.
1935	The Stroop task, which is a benchmark for selective attention, conflict and automatic processing, is developed.
1946	MRI (previously known as nuclear magnetic resonance) technique is reported independently by Felix Bloch and Edward Mills Purcell. The subsequent refinement and application of this technique in the 1970s led to the development of important assays in biological systems, such as high-resolution morphometry, diffusion tensor imaging (DTI), functional MRI (fMRI) and spectroscopy.
1951	The cognitive revolution shifts the dominant epistemology from positivism (that is, no assumptions about processes that cannot be observed directly) to realism (that is, properties exist independently of the things that manifest them).
1953	Identification of the 'cocktail party effect', which construes attention as selectively concentrating on one thing while ignoring others.
1956	Dichotic listening is developed. This involves a line of experiments in which participants listen to two auditory streams in different ears and selectively attend to one of them. Next, the experimenter poses questions concerning the unattended stream.
1958	Using terms such as 'bottleneck', Donald Broadbent construes attention as a powerful filter.
1960	Digital computers revolutionize cognitive psychology as well as laboratory data acquisition.
1962	Event-related potentials (ERPs) are used to correlate the electrical activity of the brain with specific events, usually in the context of cognitive tasks.
1968	Robert Wurtz provides neural measurements from the brains of sedated non-human primates.
1971	Michael Posner and Stephen Boies first describe different typologies of attentional subsystems.
1972	Neural correlates are recorded from the brains of behaving animals.
1977	The feature integration theory model is described by Anne Treisman. This important model suggests that attention is responsible for binding different features into a consciously experienced whole.
1980	Integration of eye-tracking in attention research following the distinction between overt and covert attention. This tool is increasingly used in attention research to measure non-verbal responses, especially with developmental and pathological populations.

of attention[19,20]. Theories of attention must also account for how these limits can be eliminated[21]. When the connections are highly practised, the bottlenecks seem to be bypassed effortlessly, and the correct action manifests. There has been relatively little research into whether it is possible to regain control over an automatic process. However, recent research provides mounting evidence that automation can indeed be reversed[21,22].

Although the study of attention generated several interesting results about the limits of performance and of unconscious processing, there was no agreement on whether attention involved separate mechanisms from those that are used to process data, let alone any analysis of what might be the neural circuits that underlie such mechanisms. Some researchers did attempt to find a unifying account of what attention was or was not, and cumulative findings supported James's idea that, rather than a monolithic concept, there might be more than one singular form of attention[23].

Favouring a three-network model of attention, this review attempts to integrate several theoretical stances that argue for separable attentional subsystems. Here, we first examine how methodological advances could identify the neural substrates of attentional control networks. Then, we review compelling evidence and discuss modern incarnations of these theories that show that the marriage of cognitive psychology to the methods of modern neuroscience improved understanding of brain mechanisms, which led to the theoretical refinement and neural localization of these ideas. Consequently, we sketch a systems-level picture of how these attentional systems operate in the brain. Finally, we consider how recent investigations of atypical attention can inform the broader theoretical integration we offer.

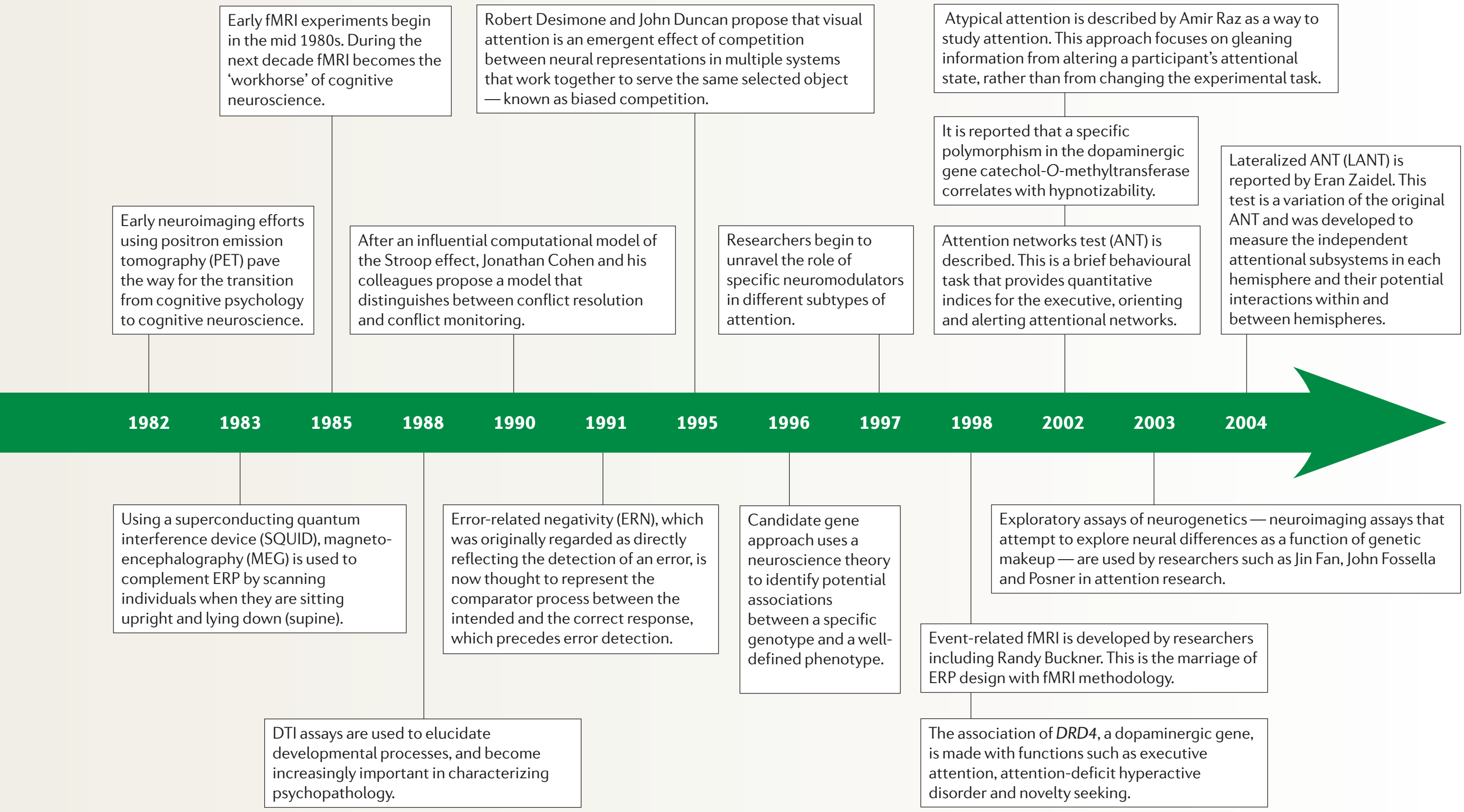
Methods of investigating attention

Although attention had already been studied from a neurophysiological view in the 1890s, Broadbent's seminal work capitalized on a single method: measuring and comparing participants' reaction times during simple cognitive tasks[24]. Chronometry of mind, together with application of the subtraction method[25], provided rich information on psychological processes[26]. In this method, reaction times from two experimental tasks were compared, with the only difference between them being that one was proposed to require an additional cognitive process. Differences in reaction time, sometimes as little as 10 ms, were taken to support and index the putative additional process. By systemically varying cognitive processing, researchers developed intricate models of brain function, many of which were subsequently supported by neuroimaging studies.

Emotional regulation
The reduction, increase or maintenance of an emotional response (for example, fear, anger or pleasure) on the basis of the actions of the self or others.

Self-regulation
The ability to manipulate one's own emotions, thoughts or actions on direction from the self or another person. Emotion regulation can be a form of self-regulation, but it can also be induced by actions of others.

Effortful control
The ability to inhibit, activate or sustain a response, which includes the capacity to inhibit a dominant response in order to perform a subdominant response. In temperament research, individual differences in effortful control are measured as a factor score that combines scales dealing with attention and the ability to regulate behaviour on command.



1982: Early neuroimaging efforts using positron emission tomography (PET) pave the way for the transition from cognitive psychology to cognitive neuroscience.

1983: Using a superconducting quantum interference device (SQUID), magnetoencephalography (MEG) is used to complement ERP by scanning individuals when they are sitting upright and lying down (supine).

1985: Early fMRI experiments begin in the mid 1980s. During the next decade fMRI becomes the 'workhorse' of cognitive neuroscience.

1988: DTI assays are used to elucidate developmental processes, and become increasingly important in characterizing psychopathology.

1990: After an influential computational model of the Stroop effect, Jonathan Cohen and his colleagues propose a model that distinguishes between conflict resolution and conflict monitoring.

1991: Error-related negativity (ERN), which was originally regarded as directly reflecting the detection of an error, is now thought to represent the comparator process between the intended and the correct response, which precedes error detection.

1995: Robert Desimone and John Duncan propose that visual attention is an emergent effect of competition between neural representations in multiple systems that work together to serve the same selected object — known as biased competition.

1996: Candidate gene approach uses a neuroscience theory to identify potential associations between a specific genotype and a well-defined phenotype.

1997: Researchers begin to unravel the role of specific neuromodulators in different subtypes of attention.

1998: Event-related fMRI is developed by researchers including Randy Buckner. This is the marriage of ERP design with fMRI methodology.

The association of *DRD4*, a dopaminergic gene, is made with functions such as executive attention, attention-deficit hyperactive disorder and novelty seeking.

2002: Attention networks test (ANT) is described. This is a brief behavioural task that provides quantitative indices for the executive, orienting and alerting attentional networks.

It is reported that a specific polymorphism in the dopaminergic gene catechol-*O*-methyltransferase correlates with hypnotizability.

Atypical attention is described by Amir Raz as a way to study attention. This approach focuses on gleaning information from altering a participant's attentional state, rather than from changing the experimental task.

2003: Exploratory assays of neurogenetics — neuroimaging assays that attempt to explore neural differences as a function of genetic makeup — are used by researchers such as Jin Fan, John Fossella and Posner in attention research.

2004: Lateralized ANT (LANT) is reported by Eran Zaidel. This test is a variation of the original ANT and was developed to measure the independent attentional subsystems in each hemisphere and their potential interactions within and between hemispheres.

Reaction time assays were later combined with mathematical formulations such as formal information theory[27,28]. However, because these methods were largely divorced from anatomical and neurobiological data, these approaches were deemed inadequate to elucidate the mechanisms whereby the human brain pays attention. In the 1950s, the advent of microelectrode recordings of single neurons from laboratory animals, at first anaesthetized but later awake, afforded examination of neurophysiological processes and supported the idea that the brain processes information in serial stages. Studies using awake monkeys revealed control systems, the terminological precursor for attentional networks, in which higher brain areas fed back their influence onto earlier processing stages[29]. This top-down effect challenged the then common view of a completely serial approach to information processing, and provided evidence for focal brain areas in the monkey parietal lobe that could be systematically related to processing operations involved in attention. These ideas were extended to humans and tested using reaction-time paradigms in patients with neuropsychological disorders[30].

The arrival of computers in the 1960s initiated the field of neuroimaging by facilitating the recording of the average electrical event-related potentials (ERPs) from scalp electrodes. Electrophysiology allowed millisecond resolution and became an ideal tool with which to explore the idea of 'attention for action' — ERPs were systematically related to sensory and motor stages of information processing[31]. In the late 1980s, neuroimaging experiments enabled the examination of activity in localized brain areas — first through the use of injected radionuclides detected by positron emission tomography (PET)[32] and later through the use of an externally imposed magnetic field in functional MRI (fMRI)[33]. During the past decade, fMRI has improved in spatial and temporal resolution, and can now provide accurate spatial information of focal brain areas that are involved in cognitive tasks, such as attention. More recently, the inferences obtained from both ERPs and magnetoencephalography (MEG), which probe perceptual processing with fine temporal detail, have been important complements to the millimetre spatial resolution of fMRI[34].

More recently, neuroimaging technology has been joined by genomics. During the past decade, the Human Genome Project has made great progress in identifying the 30,000 genes in the human genome, as well as the ~1.7 million polymorphic sites scattered across the 6 billion base-pair length of the human genome[35]. These findings hold promising prospects for illuminating how genes can influence disease development and could aid in the association of genes with particular

Inhibitory control
The reduction in the probability, speed or vigour of the normal response to a stimulus based on instruction from the self or others. It is often measured by scale scores on a questionnaire or by a task that requires one to withhold or delay a response.

Top-down effect
Controlling, regulating or overriding a stimulus-driven or other bottom-up process by such factors as attention or expectation.

Event-related potentials
(ERPs). A non-invasive electrophysiological technique based on scalp electrode recordings of evoked-response potentials.

Box 1 | Training of attention

An important development of self-regulation in children occurs between the ages of 4 and 7 years. The executive attention network develops under strong genetic control (BOX 2) but is amenable to training. A recent study conducted a 5-day training regime[130]. It was developed with the assumption that training for only a few days would be unlikely to have a large effect on behaviour, but might cause small changes that would indicate greater potential benefits of more extensive training. On the first and last days, researchers examined the children's electroencephalogram (EEG) in the attention networks test (ANT)[44], as well as their behavioural data, intelligence quotient (IQ) and temperament measures[15,16]. Findings indicate that even brief training shifts the attentional networks of children towards a more adult-like pattern. In addition, the data show that there is a striking increase in IQ, which suggests the generalization of these effects.

Similar findings have been reported in 8-year-old children diagnosed with attention-deficit hyperactivity disorder (ADHD) using computerized training of working memory[131]. After completing the training programme, children have significantly improved motor performances and IQ results on the nonverbal complex reasoning task of Raven's progressive matrices[131–133]. These findings suggest that working memory training could be of potential clinical use for improving the symptoms of ADHD. Indeed, much evidence relates working memory and executive attention, and these two concepts probably involve similar mechanisms[134]. So, similar to the above-mentioned attention training, training of working memory seems to improve the underlying neural networks and could potentially generalize to different tasks.

A more recent approach to attention training focuses on expert meditators. Complemented by recent clinical interventions[135], a long history of these practices in Eastern cultures suggests that frequent rehearsal of various attentional practices could influence cognitive and emotional experience[136]. Although the effectiveness and generalizability of these training methods are not clear, preliminary reports[119,125] suggest that meditative training could affect behaviour and brain function.

As neuroimaging begins to unravel the effects of practise on brain substrates[137,138], cumulative findings suggest that these attentional networks can be modified. Introducing attentional training in preschools or childcare centres could be an educational innovation. Moreover, exploratory findings from young individuals diagnosed with Tourette's syndrome suggests that attentional training, as well as paradigms involving atypical attention, could ameliorate symptoms of impaired impulse control and could, consequently, extend to other psychopathologies. Attention training, therefore, might be of particular importance because it fosters specific neural networks that are involved in many domains of behaviour.

psychopathologies. In addition, genomics has the potential to promote the discovery of new treatments and to afford new insights into behavioural genetics, such as the relationship between certain genetic configurations and manifest behaviour. Combining neuroimaging with genetics, recent exploratory assays endeavoured to non-invasively probe genes that have been shown to produce a variation in protein levels or biochemical activity in the context of both typical[36] and atypical[37] attention. Such pooled research efforts promise to elucidate both the neural[38] and genetic[39,40] correlates of attention.

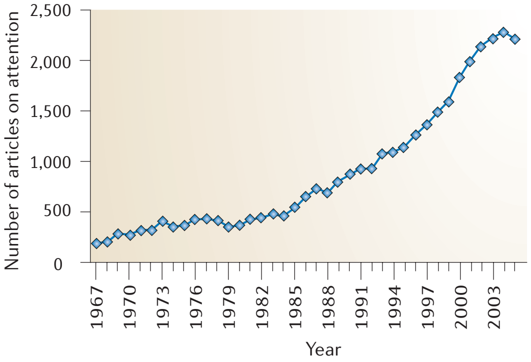


Figure 1 | **The number of research reports encompassing attention has grown in recent years.** A search of PsychInfo for articles with subject headings relating to attention reveals considerable growth in this area of research. With more than 1,500 articles published annually in recent years, adopting a big-picture approach that embraces a clear formulation of different typologies and nomenclatures would probably allow for better management of experimental findings. Such an effort would help investigators to better integrate diverse themes and approaches.

Findings from genetic and neuroimaging studies of attention have provided some convergent results. Although most neuroimaging studies yield a small number of widely distributed brain areas that must be orchestrated to carry out a cognitive task, it is often not clear what the unique contribution of each area might be. However, in the case of attention (and language), these mechanisms have been sufficiently elucidated by a careful teasing apart based on chronometry, neuroimaging and genetics. Attention, therefore, is a primary research domain, which exemplifies the links between brain and behaviour and binds psychology to the techniques of neuroscience[41].

Attentional networks

Cortical and subcortical networks mediate different aspects of attention; without the modulatory influence of subcortical areas, the brain would not attend effectively. However, for reasons of didactics and space, we focus on cortical networks and only briefly acknowledge the important contribution of subcortical circuits, such as the fronto–striato–thalamo–cortical loops. On the basis of detailed neuroanatomical, electrophysiological and neurochemical studies in animals, as well as human neuroimaging data, researchers such as Marcel Mesulam and Patricia Goldman-Rakic have identified large-scale cortical–subcortical circuits, including feedback loops and re-entrant connections, that subserve different aspects of attention and working memory.

Positron emission tomography
(PET). A technique using positron-emitting radioactive tracers that are attached to molecules that enter biological pathways of interest to study the relationship between energy consumption and neural activity.

Functional MRI
(fMRI). A non-invasive technique that permits imaging of the living brain and provides findings that relate neural to cognitive activity by measuring small changes in the magnetic properties of blood.

Magnetoencephalography
(MEG). A technique similar to ERP methods that detects the changing magnetic fields associated with brain activity.

Attention networks test
(ANT). A brief behavioural task that, together with spatiotemporal cues, assesses the efficiencies of the executive, alerting and orienting attentional networks. The ANT can be used with children or adults, in both health and disease, as well as with non-human primates.

Raven's progressive matrices
A popular measure of intellectual ability that assesses reasoning in the visual modality and provides sensitive measures of abstraction abilities. Responses do not require verbalization, skilled manipulation ability or subtle differentiation of visuospatial information.

Box 2 | Development and genetics of attention

The development of attentional networks involves both genes[39,40,139] and specific experience (BOX 1). The alerting network matures throughout adolescence and into adulthood[72]. The orienting network seems to be formed as early as 4 years of age, whereas the executive attention network shows a strong development from 4 to 7 years of age. In addition, although inhibitory control and emotional regulation development continue well into adolescence, at least some findings suggest that executive attention might not change much past the age of 7 years[72,88]. During this malleable period, the efficiency of executive control, as indexed by the attention networks test (ANT)[44], also predicts a number of behavioural and questionnaire measures of attentional regulation among normal individuals[14,15]. A recent study of children between 8 and 12 years of age showed significantly reduced brain activation in key areas associated with each of the three networks measured by the ANT: right-sided frontal-midbrain regions during alerting; right-sided temporoparietal junction during orienting; and dorsolateral prefrontal cortex during executive control of attention. The children also showed more activation in several regions compared with the adults, including the superior frontal gyrus during orienting and the superior temporal gyrus during executive control of attention, possibly indicating the use of different cognitive strategies[140].

Elucidating the role of genes in attentional networks and other cognitive networks underlying human performance is still in its infancy. Extending traditional twin studies[141], allelic association assays correlate specific genes with cognitive variation in unrelated individuals[142]. Although these effects tend to be small, by identifying brain networks and by tracing their underlying neurotransmitters, researchers have attempted to unravel links between single gene polymorphisms that influence chemical function and individual differences in cognitive function[139,141,143–145]. Initial enthusiasm has been somewhat dampened by limited progress and conflicting results. Part of the difficulty could arise from the use of distal phenotypes, such as reaction time and accuracy measures in cognitive tasks. 'Imaging genomics' — a form of genetic association analysis in which the phenotype is the physiological response of the brain that mediates a behavioural outcome — allows for a more proximal, and perhaps more discernable, association[146]. Furthermore, given a likely polygenetic involvement and complex intergene interactions, it is unlikely that studies of a single gene would be substantially revealing; ultimately, large-scale population studies will be needed to delineate these interactions.

Nonetheless, the more modest efforts pursued so far elucidate not only individual differences but the way genes could build the physical basis of the neural networks that we study. For example, extending previous reports in healthy humans[145], two neurotransmitter genes — *CHRNA4* (cholinergic receptor, nicotinic, α4) and dopamine β-hydroxylase — have been recently shown to differentially modulate the orienting and working memory systems, respectively[134]. Another example concerns the dopamine receptor D4 (*DRD4*) gene, which is important for executive attention functions, including novelty-seeking[139]; knockout mice that lack this gene explore their environment less[147]. More precise tests of attention are planned for these mice; the development of animal models for these networks could help us to describe both how genes mediate the formation of systems that are common among individuals and what alleles account for individual variability. Finally, exploratory genetic assays have also been applied in the context of atypical attention[148]. These collective findings indicate the possibility of tracing differences in the development of attention networks for children with different genotypes and attentional capacities via specific studies of gene–environment interaction and individual differences[6,18,139,149].

Allelic association assays
Experiments aimed at correlating genotype (that is, specific genetic polymorphisms) with phenotype (that is, carefully measured behaviours) in line with an underlying brain theory.

A three-network view. An early influential model, which suggested that attention has various neurological underpinnings was first proposed by Michael Posner more than 35 years ago, at a time that largely predated neuroimaging[42]. Since then — in light of new forms of data such as that from patient populations and neuroimaging — the model has been revised and refined but still retains its original tenor. That is, there are at least three key functionally and anatomically distinct types of supramodal attentional varieties[43]. Although in the early 1970s these attentional networks were termed selection, capacity and alertness, over time they have gone through a few variations[23], and today we refer to them as executive, orienting and alerting, respectively[8,44]. Imaging data largely support this model of attentional systems[45–47].

Consistent with his earlier accounts of unique attentional systems, Posner and colleagues devised a simple and brief paradigm to concurrently measure the efficiency of these attentional networks in children, adults and non-human primates. Based on results in healthy adults, they proposed that these attentional networks are largely independent[44]. They then proceeded to examine attention as an organ system that has its own functional anatomy, circuitry and cellular structure[4], and then extended these ideas to pathological conditions[3,48] and explored the influence of genetics[39,40] on these control systems.

Despite Posner's long-standing convictions, however, many researchers of attention were not immediately enamoured with his idea concerning the modularity of function in the prefrontal cortex. Consequently, it took some time and many independent studies for alternative attentional typologies to emerge[49–51]. These more recent accounts relate to the attentional trinity[52,53], and little effort has been made to contextualize these various typologies and nomenclatures into a common framework[43]. Consequently, confusion occurs as researchers apply different nomenclatures to similar meanings (for example, Posner's orienting is roughly comparable to Parasuraman's selection), or use overlapping terms in disjointed ways (for example, emotional-regulation versus self-regulation). This problem has become apparent as early information-processing views of the attention pipeline have been gradually replaced by more complex models. Attention theorists must not only clearly delineate concepts within a proposed typology, but must also precisely explain how their concepts relate to similar concepts suggested by other theorists. Acknowledging that claims of relationships among attentional networks must be resolved empirically, we sketch a big-picture approach to attention research, discussing in an overarching fashion how different findings concerning these control networks relate to and complement one another.

Typologies of attentional networks

Although researchers have traditionally highlighted the independence of attentional networks[44], these control systems cooperate and work closely together (FIG. 2). Understanding the crosstalk among these networks is important for developing a comprehensive account of attentional function. In this section, we touch on aspects of these couplings.

Alerting. Sustained attention, vigilance and alertness vaguely define the ability to increase and maintain response readiness in preparation for an impending stimulus. Specified as phasic alertness (task specific), which is distinguishable from intrinsic alertness (a general cognitive control of arousal), this capacity can be thought of as a foundational form of attention on which other attentional functions rest[49].

The efficiency of alerting is generally measured by subtracting a cue condition that gives temporal, but not location, information from a non-cue condition[44].

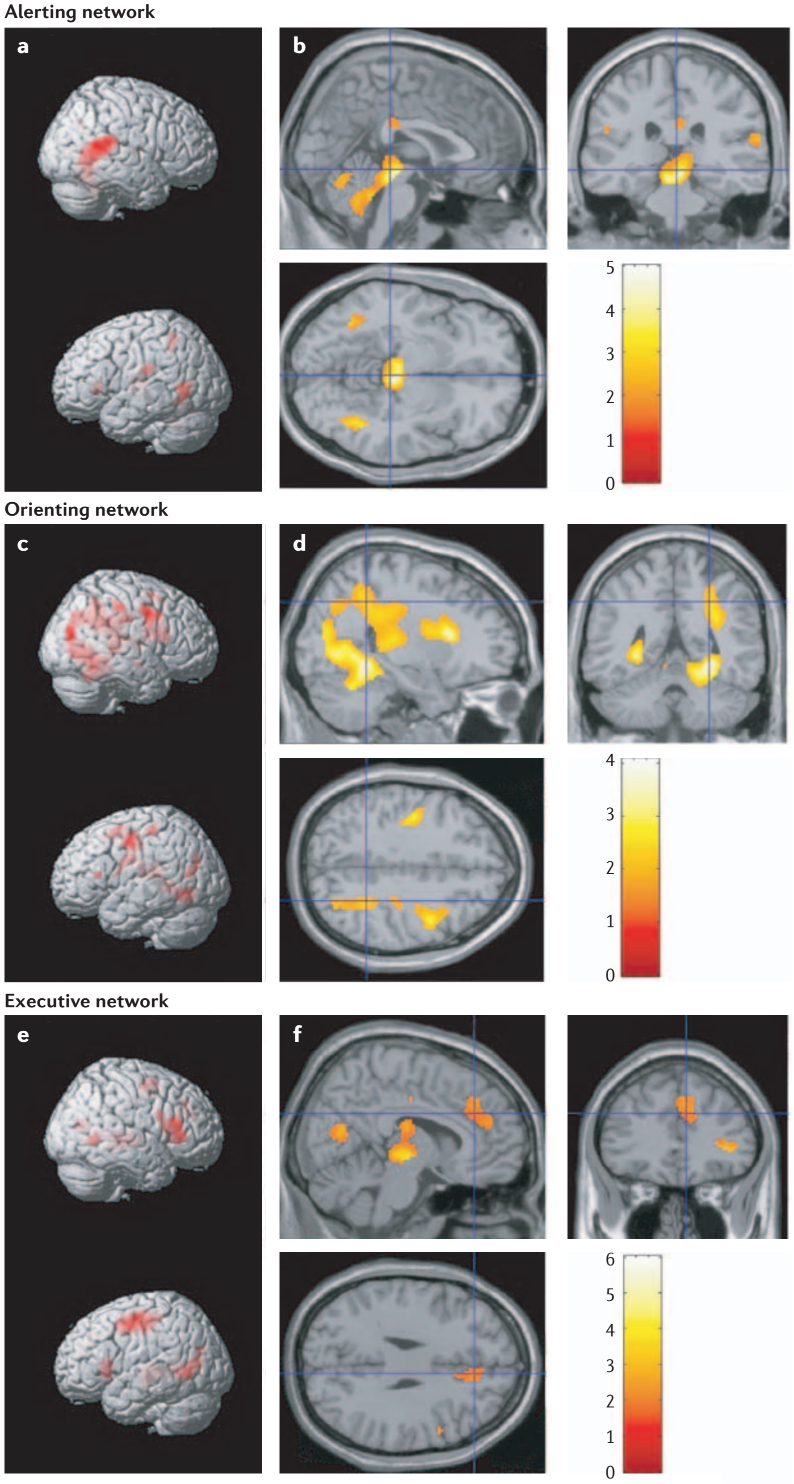


Figure 2 | **Functional activation of attentional networks.** Images of functional MRI (fMRI) scans were collected from 16 healthy adults performing the attention networks test (ANT). The panels show cross-sectional views of the three attentional networks: the alerting network shows thalamic activation (**a**), the orienting network shows parietal activation (**c**), and the conflict network shows anterior cingulated cortex activation (**e**). Panels **b**, **d** and **f** outline some of the functional anatomy subserving these distinct attentional networks. The colour 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 in one relatively short task that can be run with children and animals, as well as with adults, in both health and disease. Reproduced, with permission, from REF. 85 © (2004) Wiley InterScience.

These temporal cue tasks, which have stimulus onset asynchronies of a few seconds or less, are reminiscent of more traditional vigilance tasks, in which performance is measured by accuracy decline and reaction-time increase in the detection of small perceptual changes on a time scale of minutes or hours (FIG. 3a). Alerting tasks have largely replaced vigilance tasks in current experimental research, perhaps because of their compatibility with imaging studies[49,54]. However, some researchers challenged the supposed identity of the constructs that these two task types tap into[49].

The exact relationship between phasic alerting and intrinsic alertness (arousal) is also vague, but recent findings reveal that alertness in unwarned situations (intrinsic alertness) largely relies on a right hemisphere cortical and subcortical network in which the anterior cingulate cortex acts as the central coordinating structure[150]. From a unitary neural system modulated by the reticular formation[55], the incremental discovery of disparate arousal-regulating subsystems formed the now-accepted view that a more complex, multidimensional system governs arousal[56]. Whereas alerting typically suggests goal-directed preparedness, arousal identifies general non-specific excitability[57]. Alerting could modulate arousal via executive mechanisms in response to task demands[58]. However, the relationship between alerting and arousal is complex, and psychological variables such as stress can contribute to arousal modulation[59]. Despite efforts to explore the link between alerting and executive control, and to elucidate the difference between responding to infrequent targets and inhibiting ongoing behaviour[54], relating arousal-regulation processes to executive control and to phasic alerting remains a challenge. However, in contrast to the in-depth studies of orienting and executive control, alerting has been a rather neglected dimension of attention, and attention research has not satisfactorily elucidated its operation.

Orienting. Orienting is the ability to select specific information from among multiple sensory stimuli (sometimes known as scanning or selection), and is the most studied attentional network. Whether overt or covert (for example, with or without eye movements), orienting has traditionally been measured by reductions in reaction time to a target following a cue, which gives information on the location but not the timing of the event[60] (FIG. 3b). A distinction can be made between exogenous orienting (when the flash of a cue automatically captures attention to a specific location) and endogenous orienting (when a central arrow points to one of two lateralized target presentation locations). Unguided visual search also involves endogenous orienting[60,61]. Guided paradigms often present both valid and invalid cue trials, and reaction times in the valid condition are subtracted from those in the invalid condition to yield an efficiency score. Comparison between these two conditions and a no-cue condition usually shows a small benefit of orienting to a correctly cued location, and a larger cost for an incorrect cue.

Both endogenous (top-down) and exogenous (bottom-up) orienting enhance performance by influencing relative increases in neural activity in a given sensory system. In 'biased competition', the control system and the sensory object interact to invoke different brain systems that cooperate to ensure that the object's representation dominates across multiple neural regions[62]. For example, orienting to a particular type of target (for example, faces) or to a particular aspect of the target (for example, colour) results in activity amplification in the region where the specific task-relevant computations are carried out (for example, fusiform face area or the retinotopic visual area V4)[63,64]. This relative increase in activity can be achieved in several ways: an increase in neural response to a particular stimulus; an increase of baseline neural activity at a particular location; a reduction in the suppressive effect of distracting stimuli; and an enhancement of contrast sensitivity at a particular location[65]. The enhancement of contrast sensitivity seems to increase from early to later stages of visual processing, which suggests that the modulatory effects occur mainly in the later information-processing stages. Attention can modulate visual processing as early as the first cortical site in the visual processing stream (V1)[66], and even earlier in subcortical areas under some conditions[67], but this alteration is probably achieved indirectly by the interconnections and multiple recurrent loops that feed back from higher neural modules.

Although most research in orienting has been carried out in the visual domain, neural activity increases in response to cue and concomitant performance enhancement have been shown in most sensory systems, and some researchers have suggested that orienting could encompass not only sensory but also purely mental events, such as working memory[68]. Recent work using post-target spatial cues has shown an orienting effect for various internal representations (including items stored in working memory[69] and long-term memory[70]) and for semantic categories (T. Cristescu, J. T. Devlin and A. C. Nobre, personal communication), which suggests a considerable generalizability for orienting.

The relationship between phasic alerting and orienting remains a topic of discussion. Several behavioural studies using tasks that integrated functions of both networks demonstrated no correlation between the alerting and orienting scores, which led the authors to conclude that they are functionally distinct[44,47,71,72]. However, other studies, including our own unpublished data, have found interactions under some conditions[73]. Several rehabilitation programmes for patients with unilateral neglect, a disorder of the orienting system[74,75], involve training of the alerting system; these programmes have been shown to improve performance on neuropsychological tests and affect brain function, as measured by fMRI, which further highlights that phasic alerting and orienting do indeed interact[76,77]. In addition, it is not clear whether these two networks share a common anatomy. One recent study found greater independence[47], whereas earlier studies found greater overlap[57,78]. Finally, some researchers have argued for a heteromodal approach[69], in which at least part of the capacity subsumed by phasic alerting is conceptualized as orienting in the temporal domain[70]. Nonetheless, the

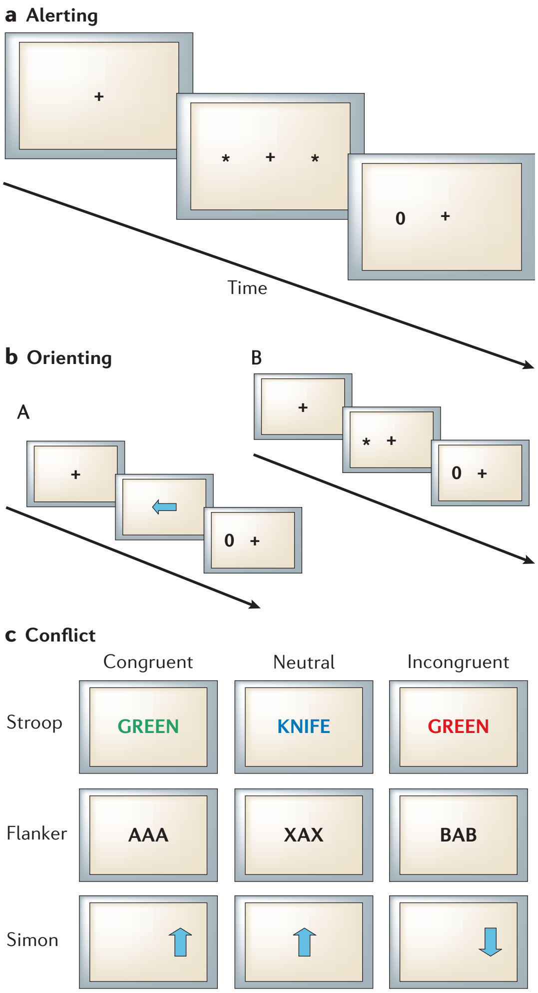


Figure 3 | **Examples of psychological tasks for studying alerting, orienting and execution. a** | In alerting tasks, participants are given a cue informing them that a target is about to appear, but they are unaware where it will appear. Even in fast-paced tasks, with targets appearing every few seconds, warning cues can greatly decrease both reaction times and error rates. **b** | In visual orienting tasks, participants fixate centrally until either an endogenous (A) or exogenous (B) cue instructs them to pay attention to a particular location where a target (for example, '0') will appear. Participants tend to show reduced reaction times and error rates to targets that have been cued. If a location is indicated by a cue but the target appears in the uncued location, longer reaction times and more errors are typical. **c** | Conflict tasks are powerful tools for studying execution function. Most of these tasks comprise congruent, neutral and incongruent conditions. The sequence of events, which is crucial for most of these designs, is displayed with cascading screen shots (represented as rectangles). Typically, reaction times, error rates and brain activity follow a pattern of congruent<neutral<incongruent. In the classic Stroop task, participants identify the ink colour in which letters are printed. In the version of the flanker task shown here, participants press one button when the centre letter is an 'A', and a second button when the centre letter is a 'B'; 'X' is not in the response set. Simon tasks rely on spatial incompatibility; in this version, participants respond by pressing a right key to an up-pointing arrow and a left key to a down-pointing arrow.

Vigilance tasks
A set of tasks requiring sustained attention during which participants typically monitor displays over extended periods of time for the occasional occurrence of crucial events (signals). Signals are low-probability events that require action, and are embedded in the context of recurrent non-signal events that require no overt response.

Alerting tasks
A set of tasks requiring participants to prepare for the imminent appearance of a target at a known location. For example, a visual cue could alert the participant that a subsequent target will soon appear at a known location.

Retinotopic visual area
Stimulating different areas of the visual field during a brain scan reveals their corresponding retinotopic representation (maps) in the cortex. Several distinct areas in visual cortex preserve the retina's map.

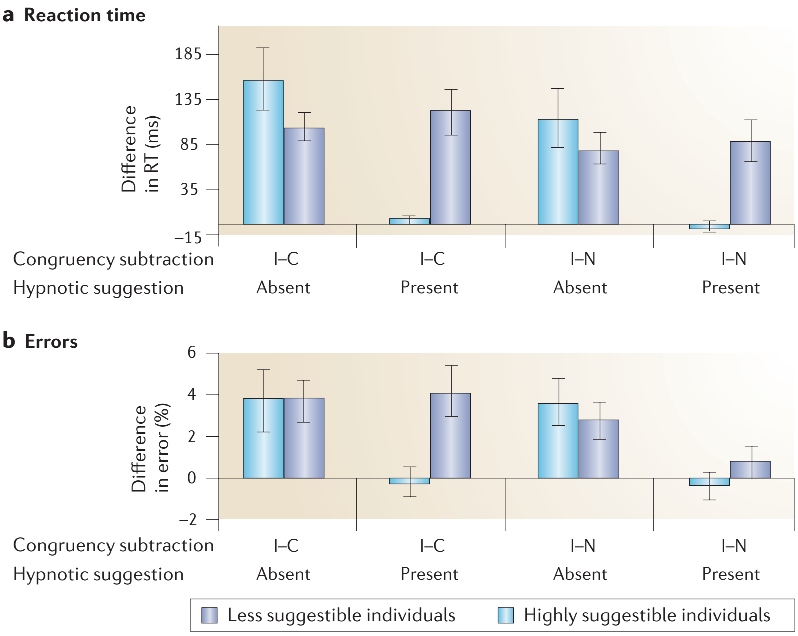


Figure 4 | **Stroop interference.** Reaction time (RT, in milliseconds; **a**) and accuracy (in percentage error; **b**) measures from 16 highly- and 16 less-suggestible participants who performed a classic Stroop task with and without a posthypnotic suggestion to obviate the Stroop effect (calculated as incongruent minus congruent trials, I–C). The suggestion, that the stimuli (that is, English Stroop words) would be meaningless scribbles written in an unfamiliar foreign language, removed Stroop interference (incongruent minus neutral, I–N) and facilitation (neutral minus congruent) in highly suggestible participants. Replication studies controlled for participants' peripheral strategies (tearing, blurring vision, squinting, averting gaze or otherwise degrading the input stream). Further investigations, with electrical recording of scalp electrodes (sitting upright) and functional MRI (lying supine) in the same participants, revealed elimination and reduction of the Stroop effect, respectively. An independent study replicated the influence of suggestion, reporting significant reduction of the Stroop effect in highly suggestible individuals. If suggestion can override what most cognitive scientists consider an automatic process (such as reading), we might need to revisit the idea of automaticity. Furthermore, the top-down influence of suggestion could have important therapeutic potential in automation reversal of other ingrained behaviours in the context of certain psychopathologies and in elucidating the neural substrates of placebo responses. For example, our pilot data from children diagnosed with Tourette's syndrome show that hypnotic suggestion can transiently ameliorate tic symptoms. The idea of testing an individual while changing their attentional efficiency with suggestion, rather than altering the experimental task, is in line with recent reports about the effects of attentional training and expert meditators. Highly hypnotizable individuals — that is, the vast majority of children and about 15% of adults — could well be excellent candidates for investigation in this new field of 'atypical attention'. Data adapted from REF 22.

bulk of the evidence supports the idea that orienting and alerting are best understood as largely disparate functions.

Executive. Executive attention goes by many names including supervisory, selective, conflict resolution and focussed attention. Developmentally, executive attention is often related to parental reports of child temperament using the term effortful control[14,79]. Some consider any instance of top-down control as executive attention, whereas others construe it as the monitoring and resolution of conflict between computations in different neural areas. These computations involve planning or decision making, error detection, new or not well-learned responses, conditions judged to be difficult or dangerous, regulation of thoughts and feelings, and the overcoming of habitual actions[18]. Executive attention is commonly measured using tasks in which there is an incompatibility between dimensions of the stimulus or response, as in the classic Stroop, flanker and Simon tasks[80–82] (FIGS 3c,4). Conflict is assessed by subtracting reaction times to congruent or neutral stimuli from those to incongruent ones.

Based on the number and detail of accounts in the literature, orienting and alerting are probably the best- and worst-specified attention networks, respectively, whereas executive attention is perhaps sandwiched between these two poles. Some researchers construe conflict as engendered at multiple levels of selective processing: Simon-like tasks measure executive attention on the basis of conflict between the irrelevant stimulus dimension and the required response, whereas Stroop-like tasks derive their effect primarily from conflict between the relevant and irrelevant stimulus dimensions[83]. Recent studies carefully compared Simon and Stroop conflicts in a single task in an attempt to dissociate stimulus–stimulus and stimulus–response conflict[84]. Findings from these studies discern between stimulus and response conflict, as well as identifying disparate neuroanatomical substrates for each[85].

The relationship between executive attention and the other attentional networks remains unclear. Several behavioural studies, which concurrently probed all three networks, found no correlation between executive scores and those of the other two networks[44,47,72]. However, other studies reported interactions under some conditions[73,86]. Attempts to relate the executive system to other cognitive concepts addresses the centrality of this network in psychological function. A good example is the relationship between executive attention and metacognition (the monitoring and control of one's own cognition). These two terms seem to describe similar functions, but have evolved independently in different research communities. Despite welcome proposals to address and unite these overlapping conceptualizations, the field has not embraced these directions[87]. A more successful effort has been the current research thrust relating developmental concepts such as emotion-regulation, self-regulation, effortful control and inhibitory control to executive attention[88]. We believe that the next step for this interdisciplinary approach is to more precisely define these concepts and their relationships. As conceptual clarity and common terminology emerge, empirical findings should be called on to test and further clarify these relationships.

Anatomy of attentional networks

The neuroanatomy and neurochemistry underlying Posner's model of attentional networks have been discussed in detail elsewhere[85]. We provide a brief sketch of this model here, and highlight a few associated concepts.

Alerting. 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 for even a brief period[54]. Recent evidence suggests that the right dorsolateral prefrontal cortex could act in a more executive capacity, monitoring performance or arousal levels and regulating them accordingly, perhaps in conjunction with the anterior cingulate cortex (ACC) or other midline frontal structures[89–91]. By contrast, the right inferior parietal region seems to participate equally in both endogenous and exogenous alerting[92].

More recently, activity in the left hemisphere has been associated with linking temporal and spatial information[93], and the specific presentation of warning signals[94]. These fMRI findings confirm the involvement of parietal and frontal sites in alerting, and they show that the specific impact of a warning cue that precedes a target by a short interval activates left hemisphere sites. One interpretation of these findings is to associate the left-hemisphere effect and the more usual right-hemisphere activation as phasic and tonic influences, respectively[47].

Orienting. The pulvinar, superior colliculus, superior parietal lobe, temporoparietal junction, superior temporal lobe and frontal eye fields are often activated in studies of the orienting network. These regions produce modality-specific effects, such as amplification in peristriate and striate regions. Different areas seem to be involved in specific subroutines in the orienting process. Lesions of the temporoparietal junction and superior temporal lobe disrupt the ability to disengage from a particular location[95,96]. The superior parietal cortex participates in voluntary, covert shifts of attention[46], whereas the frontal eye fields and superior colliculus might be primarily involved in the participation of overt eye movements in attentional shift[97].

Executive. Brain imaging studies have identified the ACC as an important node in the executive network. They have consistently demonstrated activation of the dorsal ACC (dACC) in cognitive conflict tasks[44,98], and activation in the rostral ACC (rACC) after producing an error[99]. A cognitive-affective distinction within the ACC has been widely embraced: cognitive tasks activate the dACC and deactivate the rACC, whereas affect-related tasks drive the opposite pattern[100]. However, new experimental findings suggest that this dichotomy was probably an oversimplification, and a revision would have to account for the involvement of the ACC in bodily arousal states as well as in the anticipation, evaluation and appraisal of impending stimuli[101]. In addition, whether the ACC monitors or resolves conflict is not clear. Expanding on their initial formal model of Stroop conflict[102], Cohen and colleagues proposed a conflict-monitoring model that obviates the proverbial homunculus, suggesting that the ACC engages the dorsolateral prefrontal cortex (DLPFC), which might be mediated by the locus coeruleus and dopaminergic sites in the ventral tegmental area[103,104]. By contrast, the conflict resolution view argues that the ACC can subserve both functions directly[100]. Whether the ACC resolves or simply monitors conflict, its function seems to preferentially relate to conflict at the response, rather than stimulus, level. This is supported by a recent neuroimaging assay that carefully compared Simon and Stroop conflicts in a single task[84], as well as by several other studies that attempted to dissociate stimulus–stimulus from stimulus–response conflict[105,106]. Furthermore, these findings suggest that the DLPFC might support heteromodal conflict resolution, whereas the ACC could be specific to the resolution of response conflict.

Neuromodulators. Pharmacological findings draw on the work of luminaries such as Richard Marrocco, Trevor Robbins, Martin Sarter and Gary Aston-Jones. Their research related each of these networks to specific chemical neuromodulators. The noradrenaline system, which arises in the locus coeruleus of the midbrain, functions in alerting. The cholinergic system, which arises in the basal forebrain, has an important role in orienting through its effects in the parietal cortex[107], where it seems to reduce neural activity and reaction time cost associated with cueing to an invalid target[108]. The ACC and lateral prefrontal cortex are involved in executive attention, and are target areas of the mesocortical dopamine system. Highlighting the complex interactions between these systems, a recent study found that the cholinergic agonist nicotine modulated reaction time and brain activity associated with orienting, as would be expected; although alerting reaction time was not affected, changes in associated neural activity were observed.

Atypical attention

Several human practices, such as drug ingestion, meditation and hypnosis, can dramatically influence attention[8]. Cognitive neuroscientists are beginning to unravel the ways in which these routines influence the human brain and how such effects alter common information processing[21,109]. It is possible to test the limits of attentional functions by examining healthy individuals under atypical conditions[110]. Social psychologists have successfully used this research model, recruiting such tools as suggestion and deception to their research arsenal[111]. However, although researchers in social psychology can ‘push’ healthy participants towards the pathological spectrum in their efforts to illuminate behaviour, cognitive neuroscientists have shied away from this approach, focusing instead on patients with specific brain lesions to understand the nonpathological brain. That more research should focus on the investigation of the neuropsychological domain of healthy individuals is evident in light of the contributions of social psychology to cognitive science and exploratory assays of evanescent attention deficits, as well as the impact of reversible lesion research on cognitive science using transcranial magnetic stimulation (TMS)[58,112].

Cognitive neuroscientists generally agree that mental processes come in two varieties — controlled and automatic[19]. Some processes are thought to be innately automatic; others become automatic through practise[20]. General accounts speculate that once automated, these processes are initiated unintentionally, effortlessly, even ballistically, and cannot be easily interrupted or prevented[19,20]. For example, the Stroop effect suggests that reading words is an automatic process for a proficient reader[82]. The standard account proposes that words are

Proverbial homunculus
A term of art in neuroscience. Homunculus refers to the ‘little man’ inside the brain.

Transcranial magnetic stimulation
(TMS). A technique used to induce transient interruption of normal activity in a relatively restricted area of the brain by rapidly changing a strong magnetic field near the brain area of interest.

processed automatically at the semantic level and that the Stroop effect is the 'gold standard' of automated performance[82]. Although cognitive scientists have focused on the processes that lead to automation, with more than 4,000 citations of Stroop's original work alone[82], the question of whether it is possible to regain control over an automatic process is unanswered, and rarely asked. However, mounting evidence from assays of atypical attention shows that reversal of automation is possible. A few meditative practices claim to achieve such a reversal[113] with some sparse evidence of reduced Stroop interference[114,115]. The most compelling findings that shed light on this issue were recently used to show that a specific posthypnotic suggestion reduced and even removed Stroop interference in highly hypnotizable participants[21,22,110,116]. Reduction of the Stroop effect occurred after a reduction in ACC activation and altered processing in an occipito-parietal location that might be related to the chunking of visual letters into words[21,110]. Independent accounts under typical conditions also challenge the robustness of the Stroop effect[117]. Although critiqued[118], interpretation of these and other results supports the idea that attention can be used to derail automatic processes.

Other demonstrations of top-down modulation and reversal of automation showed that following hypnotic instruction to view a coloured picture as greyscale, highly hypnotizable participants showed reduced activity in colour areas of the prestriate cortex[109]. Results from these studies, together with recent preliminary data we have collected using classic visual search paradigms, show that atypical attention can influence at least executive attention and possibly some of the other attentional networks. Exploratory assays using other forms of atypical attention could further elucidate the malleability of attentional networks[119]. For example, meditation training could be a way to induce a long-term baseline change in attentional function (BOX 1).

Conclusions and future research

Attention as a unitary idea has been researched for more than a century. The recent surge in the number of attention-related reports has been impressive, even when considering the general wave that cognitive science research has been riding. The result has been a fragmentation, rather than consolidation, of attention into highly specialized yet isolated subfields that are perhaps difficult to unify. However, converging data from behavioural, imaging, electrical scalp recording, developmental, and genetic assays provide compelling evidence for the existence of different attentional networks.

Although disparate modules of attention constitute an important model, the exact nature of these networks and the degree to which they are independent is still not clear. Although independence can occur under some conditions[44], lack of statistical correlation among the attentional networks, especially during development (BOX 2), could reflect unreliability rather than independence. Replication attempts using similar, but not identical, tasks have since challenged this putative independence[73,86], which is consistent with another toned-down account[47]. Nonetheless, the merit of construing several supramodal control networks for attention, instead of one monolithic system, does not hinge on their statistical independence but rather on how they are conceptually and neurally operated.

Although influential, Posner's account is but one model of attention. Other prominent researchers, including associates of Posner, hold different views about the functions and mechanisms of attention. For example, both Robert Desimone and John Duncan oppose Posner's earlier idea of a fast moving attentional spotlight that is controlled by the parietal cortex[120]. Posner coined his idea of a 'spotlight of attention' more as a helpful metaphor than a literal analogy; some investigators have even sought to characterize the physical properties of this elusive spotlight. However, Duncan suggests a much slower mechanism mediated by the prefrontal cortex, and Desimone postulates an important opposing theory to Posner's spotlight theory — the neural competition theory — that has gained considerable support both experimentally and from researchers in the field. In addition, excellent accounts by Leslie Ungerleider and colleagues[62,65,121], as well as findings reported by Maurizio Corbetta and Gordon Shulman, pave the way for a better understanding of the orienting subsystem, especially with regard to the distinction between endogenous and exogenous orienting[122–124]. Taken together, these dissimilar accounts complement each other in that their extensions, revisions and interactions propel the refinement of theoretical models and testable predictions, although unresolved differences do persist.

Attention is a good model system for testing the genetics of cognition because we have data about the brain systems and their associated neurochemical innervation. By targeting candidate genes that are consistent with theories of brain function and by considering the appropriate cognitive function as phenotype, several exploratory studies have reported associations between genes and cognitive functions on the basis of modest samples of healthy participants (BOX 2). The promise of this method is evident in exploratory findings that suggest a way to discern attention from working memory and from individuals with high or low levels of suggestibility.

The study of atypical conditions has paved the way for an important new avenue for attention research. Findings from such assays suggest new research directions for studying attention under extreme conditions, albeit evanescent, elucidating the health–pathology continuum, and adopting experimental designs that have, until now, been unexplored in the cognitive neuroscience of attention. For example, the innovation of recent demonstrations using hypnotic suggestion is that they maintained the experimental design and instead manipulated the participants' attention[110]. Extensive attention training, such as that seen in those that are experts at meditation, who can rapidly and volitionally invoke alternate attention profiles, could also permit exciting investigations of the regulation of actions and emotions[125].

Although alerting seems to be a foundational attentional network, supporting the function of attention globally, it has been understudied. Investigation of the alerting system could be particularly important because it might potentiate the efficiency of other networks.

Posthypnotic suggestion
A condition during common wakefulness (after termination of the hypnotic experience) during which, on a prearranged cue, a participant readily complies with a suggestion made during the hypnotic episode.

Because alerting in the laboratory is likely to be very different from alerting to real danger, general performance in the psychology laboratory might not be indicative of its ecological validity (for example, due to such factors as motivation). It is not always clear, therefore, whether and how laboratory experiments, especially neuroimaging assays, might be generalized to real-life situations[126]. In addition, either dampening down or boosting the efficiency of the alerting network could alter the participant's mental readiness, and so facilitate the phenomenon of atypical attention.

The concept of an attentional network seems to serve a heuristic purpose because researchers can make predictions about new studies. For example, if attentional networks are orthogonal, we can use atypical attention to influence one network but not another. According to Karl Popper, one of the greatest philosophers of science in the twentieth century, a proposition or theory is truly scientific, as opposed to non-scientific or pseudo-scientific, if it allows the possibility of being shown false — the falsifiability criterion. It is not clear, however, whether the attentional network theory is falsifiable in the Popperian sense: if independence is observed, then it can be attributed to the fact that the networks underlying these components do not interact; but if an interaction is observed, as in the findings of Robertson and Driver on neglect and alerting[127], the result can be attributed to network overlap, which is an explicit part of Robertson's typology.

Research with patients with neglect has elucidated how attentional networks (for example, alerting and orienting) can interact to influence one another[96,128], but findings from healthy participants have been just as compelling[129]. Indeed, because attentional control networks have unique components but also at least some overlapping substrates, one can argue for either a degree of independence or dependence, respectively. Therefore, opposing results can be explained by the same network theory. However, the history of science reveals that many theories were not initially falsifiable, not because they were not sufficiently well operationalized in terms of measurable variables (for example, in the case of Freudian theories), but because they were not fully developed. Nevertheless, such theories served a valuable heuristic purpose and Posner's three-network theory is a good example of such an all-encompassing theory: it has generated a large body of useful research from which new theories and empirical findings have evolved. Furthermore, it could well be that this theory will be extended and revised to permit more testable predictions as additional research is conducted using new methodologies (BOXES 1,2). The three-network theory is a valuable model in that it directs us towards discovery, albeit of an attentional system that requires further elucidation.

A glimpse into memory research and its terminological disarray suggests that it is also unrealistic to expect a consensus to prevail about a common taxonomy for attention, not to mention its components or its underlying terminology. However, if clinicians and researchers start speaking of attentional varieties, rhetorically as well as conceptually, we could witness considerable advances. As research tools become progressively more accessible, attention is likely to provide insights into many aspects of human behaviour and further integrate the psychological and brain sciences[7]. We hope that the importance of conceptual tools receives priority as information rapidly accumulates. A cogent account of different typologies and nomenclatures would allow for better management of experimental findings, guide future research agendas and help to shape the quest to unravel human attention.

1. Raz, A. in *Encyclopedia of Applied Psychology* (ed. Spielbereger, C.) 203–208 (Elsevier Science, San Diego, California, 2004).
2. Posner, M. I. & Rothbart, M. K. Influencing brain networks: implications for education. *Trends Cogn. Sci.* **9**, 99–103 (2005).
3. Clarkin, J. F. & Posner, M. Defining the mechanisms of borderline personality disorder. *Psychopathology* **38**, 56–63 (2005).
4. Posner, M. I. & Fan, J. in *Topics in Integrative Neuroscience: From Cells to Cognition* (eds Pomerantz, J. R. & Crai, M. C.) (Cambridge Univ. Press, Cambridge, UK, in the press).
5. Rueda, M. R., Rothbart, M. K., McCandliss, B. D., Saccomanno, L. & Posner, M. I. Training, maturation, and genetic influences on the development of executive attention. *Proc. Natl Acad. Sci. USA* **102**, 14931–14936 (2005).
Shows how even a brief period of attentional training can improve performance in children.
6. Mayr, U., Awh, E. & Keele, S. W. *Developing Individuality in the Human Brain: a Tribute to Michael I. Posner* (APA, Washington, DC, 2005).
A recent volume written in honour of Posner before his retirement and in light of his Tenth Annual George A. Miller Distinguished Lecture (presented at the Annual Meeting of the Cognitive Neuroscience Society in the spring of 2004). This book focuses on aspects of attention, such as individual differences, emotional regulation, effortful control and the potential of using attentional training and genetics to alter and elucidate phenotype, respectively.
7. Posner, M. I. & Rothbart, M. K. Hebb's neural networks support the integration of psychological science. *Can. Psychol.* **45**, 265–278 (2004).
8. Fan, J., Raz, A. & Posner, M. I. in *Encyclopedia of Neurological Sciences* (eds Aminoff, M. J. & Daroff, R. B.) 292–299 (Elsevier Science, New York, 2003).
9. James, W. *The Principles of Psychology* (Dover, New York, 1890).
One of the early texts, and still one of the most insightful, to address the psychology of attention. James conflated attention with awareness, defining it as "the taking possession of the mind in clear and vivid form of one out of what seem several simultaneous objects or trains of thought".
10. Mirsky, A. F., Anthony, B. J., Duncan, C. C., Ahearn, M. B. & Kellam, S. G. Analysis of the elements of attention: a neuropsychological approach. *Neuropsychol. Rev.* **2**, 109–145 (1991).
11. Broadbent, D. E. *Perception and Communication* (Pergamon, New York, 1958).
A classic book detailing Broadbent's idea of attention as a filter, which guided research for many years.
12. Treisman, A. in *The Cognitive Neurosciences III* (ed. Gazzaniga, M. S.) 529–544 (MIT Press, New York, 2004).
13. Posner, M. I. & Rothbart, M. K. Attention, self-regulation and consciousness. *Phil. Trans. R. Soc. Lond. B* **353**, 1915–1927 (1998).
14. Posner, M. I. & Rothbart, M. K. Developing mechanisms of self-regulation. *Dev. Psychopathol.* **12**, 427–441 (2000).
15. Rothbart, M. K., Ellis, L. K. & Posner, M. I. in *Handbook of Self Regulation* (eds Baumeister, R. F. & Vohs, K. D.) 357–370 (Guilford, New York, 2004).
16. Rothbart, M. K., Ellis, L. K., Rueda, M. R. & Posner, M. I. Developing mechanisms of temperamental effortful control. *J. Pers.* **71**, 1113–1143 (2003).
Outlines the idea of effortful control as applied to attention and emotional regulation.
17. Durston, S. *et al*. A neural basis for development of inhibitory control. *Dev. Sci.* **5**, 9–16 (2002).
18. Posner, M. I. *Cognitive Neuroscience of Attention* (Guilford, New York, 2004).
One of the most recent volumes on the cognitive neuroscience of attention. This textbook includes contributions from many prominent researchers who both side with and oppose Posner's influential three-network model.
19. Schneider, W. & Shiffrin, R. M. Controlled and automatic human information processing: I. Detection, search and attention. *Psychol. Rev.* **84**, 1–66 (1977).
20. Spelke, E., Hirst, W. & Neisser, U. Skills of divided attention. *Cognition* **4**, 215–230 (1976).
21. Raz, A., Fan, J. & Posner, M. I. Hypnotic suggestion reduces conflict in the human brain. *Proc. Natl Acad. Sci. USA* **102**, 9978–9983 (2005).
A converging data (behavioural, ERP and fMRI) approach to how atypical attention can inform basic research questions: a posthypnotic suggestion to construe words as nonsense strings reduces Stroop conflict.

22. Raz, A., Shapiro, T., Fan, J. & Posner, M. I. Hypnotic suggestion and the modulation of Stroop interference. *Arch. Gen. Psychiatry* **59**, 1155–1161 (2002).
23. Posner, M. I. & Petersen, S. E. The attention system of the human brain. *Annu. Rev. Neurosci.* **13**, 25–42 (1990).
    A seminal paper describing an earlier version of Posner's attentional trinity.
24. Posner, M. I. Timing the brain: mental chronometry as a tool in neuroscience. *PLoS Biol.* **3**, e51 (2005).
25. Donders, F. C. On the speed of mental processes. *Acta Psychol. (Amst.)* **30**, 412–431 (1969).
    One of the earliest accounts of the subtraction method in psychology.
26. Posner, M. I. Chronometric explorations of mind (L. Erlbaum Associates, Hillsdale, New Jersey, 1978).
27. Shannon, C. E. & Weaver, W. The mathematical theory of communication (Univ. of Illinois Press, Urbana, Illinois, 1949).
28. Posner, M. I. Components of skilled performance. *Science* **152**, 1712–1718 (1966).
29. Mountcastle, V. B. Brain mechanisms for directed attention. *J. R. Soc. Med.* **71**, 14–28 (1978).
30. Posner, M. I. in *Master Lectures in Clinical Neuropsychology and Brain Function: Research, Measurement, and Practice* (eds Boll, T. & Bryant, B.) 171–202 (American Psychological Association, Washington DC, 1988).
31. Luck, S. J. & Girelli, M. in *The Attentive Brain* (ed. Parasuraman, R.) 71–94 (MIT Press, Cambridge, Massachusetts, 1998).
32. Posner, M. I. & Raichle, M. E. *Images of Mind* (revised) (Scientific American Books, Washington DC, 1996).
33. Rosen, B. R., Buckner, R. L. & Dale, A. M. Event-related functional MRI: past, present, and future. *Proc. Natl Acad. Sci. USA* **95**, 773–780 (1998).
34. Hopfinger, J. B., Luck, S. J. & Hillyard, S. A. in *The Cognitive Neurosciences III* (ed. Gazzaniga, M. S.) 561–574 (MIT Press, Cambridge, Massachusetts, 2004).
35. Wolfsberg, T. G., Wetterstrand, K. A., Guyer, M. S., Collins, F. S. & Baxevanis, A. D. A user's guide to the human genome. *Nature Genet.* **32** (Suppl.), 1–79 (2002).
36. Fan, J., Fossella, J., Sommer, T., Wu, Y. & Posner, M. I. Mapping the genetic variation of executive attention onto brain activity. *Proc. Natl Acad. Sci. USA* **100**, 7406–7411 (2003).
37. Raz, A. Attention and hypnosis: neural substrates and genetic associations of two converging processes. *Int. J. Clin. Exp. Hypn.* **53**, 237–258 (2005).
38. Posner, M. I. in *Attention and Performance XX* (eds Kanwisher, N. & Duncan, J.) 505–528 (Oxford Univ. Press, New York, 2004).
39. Fossella, J., Posner, M. I., Fan, J., Swanson, J. M. & Pfaff, D. W. Attentional phenotypes for the analysis of higher mental function. *Scientific World* **2**, 217–223 (2002).
40. Fossella, J. *et al.* Assessing the molecular genetics of attention networks. *BMC Neurosci.* **3**, 14 (2002).
41. Posner, M. I. Imaging a science of mind. *Trends Cogn. Sci.* **7**, 450–453 (2003).
42. Posner, M. I. & Boies, S. J. Components of attention. *Psychol. Rev.* **78**, 391–408 (1971).
43. Robertson, I. H. in *Cognitive Neuroscience of Attention* (ed. Posner, M. I.) 407–419 (Guilford, New York, 2004).
44. Fan, J., McCandliss, B. D., Sommer, T., Raz, A. & Posner, M. I. Testing the efficiency and independence of attentional networks. *J. Cogn. Neurosci.* **14**, 340–347 (2002).
    A behavioural paradigm that provides a concurrent measure of the three attentional subsystems, and that has consequently been broadly used by attention researchers.
45. Hopfinger, J. B., Buonocore, M. H. & Mangun, G. R. The neural mechanisms of top-down attentional control. *Nature Neurosci.* **3**, 284–291 (2000).
46. Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P. & Shulman, G. L. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neurosci.* **3**, 292–297 (2000).
47. Fan, J., McCandliss, B. D., Fossella, J., Flombaum, J. I. & Posner, M. I. The activation of attentional networks. *Neuroimage* **26**, 471–479 (2005).
    A fMRI assay showing the neural substrates that subserve the attentional networks. This report provides a slightly different take on the independence of these attentional subsystems and paves the road to further refinement of the three-network model.
48. Posner, M. I. *et al.* Attentional mechanisms of borderline personality disorder. *Proc. Natl Acad. Sci. USA* **99**, 16366–16370 (2002).
49. Parasuraman, R., Warm, J. & See, J. in *The Attentive Brain* (ed. Parasuraman, R.) 221–256 (MIT Press, Cambridge, Massachusetts, 1998).
50. Robertson, I. H. & Garavan, H. in *The New Cognitive Neurosciences* (ed. Gazzaniga, M. S.) 631–640 (MIT Press, New York, in the press).
51. Washburn, D. A. John Merk Fund Summer Institute on the Biology of Developmental Disabilities July 18–23 2004 (Princeton University, New Jersey, USA).
52. Robertson, I. H., Ward, T., Ridgeway, V. & Nimmo-Smith, I. The structure of normal human attention: the Test of Everyday Attention. *J. Int. Neuropsychol. Soc.* **2**, 525–534 (1996).
    Preceding the ANT, the Test of Everyday Attention was pioneered by Ian Robertson (a well-known attention 'typologist') and colleagues, and is one of the more ecological ways to measure attention.
53. Manly, T. *et al.* The differential assessment of children's attention: the Test of Everyday Attention for Children (TEA-Ch), normative sample and ADHD performance. *J. Child Psychol. Psychiatry* **42**, 1065–1081 (2001).
54. Robertson, I. H. & Garavan, H. in *The Cognitive Neurosciences III* (ed. Gazzaniga, M. S.) 631–640 (MIT Press, New York, 2004).
55. Moruzzi, G. & Magoun, H. W. Brain stem reticular formation and activation of the EEG. *Electroenceph. Clin. Neurophysiol.* **1**, 455–473 (1949).
56. Olszewski, J. B. D. *Cytoarchitecture of the Human Brain Stem* (Karger, Basel, 1982).
57. Sturm, W. & Willmes, K. On the functional neuroanatomy of intrinsic and phasic alertness. *Neuroimage* **14**, S76–S84 (2001).
58. Raz, A., Deouell, L. Y. & Bentin, S. Is pre-attentive processing compromised by prolonged wakefulness? Effects of total sleep deprivation on the mismatch negativity. *Psychophysiology* **38**, 787–795 (2001).
59. Broadbent, D. E. *Decision and Stress* (Academic, London, 1971).
60. Posner, M. I. Orienting of attention. *Q. J. Exp. Psychol.* **32**, 3–25 (1980).
    Posner's Cueing Task, one of the most widely used paradigms in attentional research.
61. Treisman, A. M. & Gelade, G. A feature-integration theory of attention. *Cogn. Psychol.* **12**, 97–136 (1980).
62. Kastner, S. & Ungerleider, L. G. The neural basis of biased competition in human visual cortex. *Neuropsychologia* **39**, 1263–1276 (2001).
63. Carmel, D. & Bentin, S. Domain specificity versus expertise: factors influencing distinct processing of faces. *Cognition* **83**, 1–29 (2002).
64. Corbetta, M., Miezin, F. M., Dobmeyer, S., Shulman, G. L. & Petersen, S. E. Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *J. Neurosci.* **11**, 2383–2402 (1991).
65. Kastner, S. & Ungerleider, L. G. Mechanisms of visual attention in the human cortex. *Annu. Rev. Neurosci.* **23**, 315–341 (2000).
    One of the more comprehensive reviews of attention focusing on alternative models to that described by Posner.
66. Martinez, A. *et al.* Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neurosci.* **2**, 364–369 (1999).
    A compelling demonstration that attention can modulate activity very early in the neural processing stream.
67. Kastner, S. *et al.* Functional imaging of the human lateral geniculate nucleus and pulvinar. *J. Neurophysiol.* **91**, 438–448 (2004).
68. Desimone, R. Visual attention mediated by biased competition in extrastriate visual cortex. *Phil. Trans. R. Soc. Lond. B* **353**, 1245–1255 (1998).
    A description of the biased competition model.
69. Griffin, I. C. & Nobre, A. C. Orienting attention to locations in internal representations. *J. Cogn. Neurosci.* **15**, 1176–1194 (2003).
70. Summerfield, J. J., Lepsien, J., Gitelman, D. R., Mesulam, M. M. & Nobre, A. C. Orienting attention based on long-term memory experience. *Neuron* **49**, 905–916 (2006).
71. Fernandez-Duque, D. & Posner, M. I. Relating the mechanisms of orienting and alerting. *Neuropsychologia* **35**, 477–486 (1997).
72. Rueda, M. R. *et al.* Development of attentional networks in childhood. *Neuropsychologia* **42**, 1029–1040 (2004).
73. Callejas, A., Lupianez, J. & Tudela, P. The three attentional networks: on their independence and interactions. *Brain Cogn*. **54**, 225–227 (2004).
74. Halligan, P. W., Fink, G. R., Marshall, J. C. & Vallar, G. Spatial cognition: evidence from visual neglect. *Trends Cogn. Sci.* **7**, 125–133 (2003).
75. Karnath, H. O., Fruhmann Berger, M., Kuker, W. & Rorden, C. The anatomy of spatial neglect based on voxelwise statistical analysis: a study of 140 patients. *Cereb. Cortex* **14**, 1164–1172 (2004).
76. Robertson, I. H., Tegner, R., Tham, K., Lo, A. & Nimmo-Smith, I. Sustained attention training for unilateral neglect: theoretical and rehabilitation implications. *J. Clin. Exp. Neuropsychol.* **17**, 416–430 (1995).
77. Thimm, M., Fink, G. R., Kust, J., Karbe, H. & Sturm, W. Impact of alertness training on spatial neglect: A behavioural and fMRI study. *Neuropsychologia* 6 Nov 2005 (doi:10.1016/j.neuropsychologia.2005.09.008).
78. Griffin, I. C., Miniussi, C. & Nobre, A. C. Orienting attention in time. *Front. Biosci.* **6**, D660–D671 (2001).
79. Posner, M. I. *et al.* An approach to the psychobiology of personality disorders. *Dev. Psychopathol.* **15**, 1093–1106 (2003).
80. Eriksen, B. A. & Eriksen, C. W. Effects of noise letters upon the identification of a target letter in a nonsearch task. *Percept. Psychophys.* **16**, 143–149 (1974).
81. Simon, J. R. Reactions toward the source of stimulation. *J. Exp. Psychol.* **81**, 174–176 (1969).
82. Stroop, J. R. Studies of interference in serial verbal reactions. *J. Exp. Psychol.* **18**, 643–661 (1935).
    The original Stroop paper — the most cited paper in the history of experimental psychology.
83. Kornblum, S. in *Tutorials in Motor Behavior II* (ed. Stelmach, G. E. & Requin, J.) 743–777 (Elsevier Science, Amsterdam, 1992).
84. Liu, X., Banich, M. T., Jacobson, B. L. & Tanabe, J. L. Common and distinct neural substrates of attentional control in an integrated Simon and spatial Stroop task, as assessed by event-related fMRI. *Neuroimage* **22**, 1097–1106 (2004).
    An important report delineating subtle methodological influences that could account for differences between Simon and Stroop results.
85. Raz, A. Anatomy of attentional networks. *Anat. Rec. B New. Anat.* **281**, 21–36 (2004).
    An overview of the main anatomy and the underlying theory proposing a three-network model for attention.
86. Funes, M. J. & Lupiáñez, J. La teoría atencional de Posner: una tarea para medir las funciones atencionales de orientación, alerta y control cognitivo y la interacción entre ellas. *Psicothema* **15**, 260–266 (2003).
87. Fernandez-Duque, D., Baird, J. A. & Posner, M. I. Executive attention and metacognitive regulation. *Conscious Cogn.* **9**, 288–307 (2000).
88. Rueda, M. R., Posner, M. I. & Rothbart, M. K. in *Handbook of Self Regulation* (eds Baumeister, R. F. & Vohs, K. D.) 283–300 (Guilford, New York, 2004).
89. Critchley, H. D. *et al.* Human cingulate cortex and autonomic control. *Brain* **126**, 2139–2152 (2003).
90. Critchley, H. D., Melmed, R. N., Featherstone, E., Mathias, C. J. & Dolan, R. J. Brain activity during biofeedback relaxation: a functional neuroimaging investigation. *Brain* **124**, 1003–1012 (2001).
91. Critchley, H. D., Melmed, R. N., Featherstone, E., Mathias, C. J. & Dolan, R. J. Volitional control of autonomic arousal: a functional magnetic resonance study. *Neuroimage* **16**, 909–919 (2002).
92. O'Connor, C., Manly, T., Robertson, I. H., Hevenor, S. J. & Levine, B. An fMRI study of sustained attention with endogenous and exogenous engagement. *Brain Cogn.* **54**, 133–135 (2004).
93. Assmus, A., Marshall, J. C., Noth, J., Zilles, K. & Fink, G. R. Difficulty of perceptual spatiotemporal integration modulates the neural activity of left inferior parietal cortex. *Neuroscience* **132**, 923–927 (2005).
94. Coull, J. T., Nobre, A. C. & Frith, C. D. The noradrenergic $\alpha 2$ agonist clonidine modulates behavioural and neuroanatomical correlates of human attentional orienting and alerting. *Cereb. Cortex* **11**, 73–84 (2001).
95. Friedrich, F. J., Egly, R., Rafal, R. D. & Beck, D. Spatial attention deficits in humans: a comparison of superior parietal and temporal–parietal junction lesions. *Neuropsychology* **12**, 193–207 (1998).

96. Karnath, H. O., Ferber, S. & Himmelbach, M. Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature* **411**, 950–953 (2001).
97. Corbetta, M. Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems? *Proc. Natl Acad. Sci. USA* **95**, 831–838 (1998).
An alternative to the idea of independent attention subsystems. This research nicely complements Posner's model and extends aspects of the orienting system.
98. Fan, J., Flombaum, J. I., McCandliss, B. D., Thomas, K. M. & Posner, M. I. Cognitive and brain consequences of conflict. *Neuroimage* **18**, 42–57 (2003).
99. Pizzagalli, D. A., Peccoralo, L. A., Davidson, R. J. & Cohen, J. D. Resting anterior cingulate activity and abnormal responses to errors in subjects with elevated depressive symptoms: a 128-channel EEG study. *Hum. Brain Mapp.* **27**,185–201 (2006).
100. Bush, G., Luu, P. & Posner, M. I. Cognitive and emotional influences in anterior cingulate cortex. *Trends Cogn. Sci.* **4**, 215–222 (2000).
An influential review, albeit in need of revision in light of recent evidence, that argues for a superior cognitive and inferior emotional regulation system in the anterior cingulate cortex.
101. Critchley, H. D. *et al*. Human cingulate cortex and autonomic control: converging neuroimaging and clinical evidence. *Brain* **126**, 2139–2152 (2003).
102. Cohen, J. D., Aston-Jones, G. & Gilzenrat, M. S. in *Cognitive Neuroscience of Attention* (ed. Posner, M. I.) 71–90 (Guilford, New York, 2004).
103. Botvinick, M. M., Cohen, J. D. & Carter, C. S. Conflict monitoring and anterior cingulate cortex: an update. *Trends Cogn. Sci.* **8**, 539–546 (2004).
104. Kerns, J. G. *et al*. Anterior cingulate conflict monitoring and adjustments in control. *Science* **303**, 1023–1026 (2004).
105. Milham, M. P. *et al*. The relative involvement of anterior cingulate and prefrontal cortex in attentional control depends on nature of conflict. *Brain Res. Cogn. Brain Res*. **12**, 467–473 (2001).
106. van Veen, V. & Carter, C. S. Separating semantic conflict and response conflict in the Stroop task: a functional MRI study. *Neuroimage* **27**, 497–504 (2005).
107. Schulte, D. *et al*. Propofol decreases stimulated dopamine release in the rat nucleus accumbens by a mechanism independent of dopamine D_2, $GABA_A$ and NMDA receptors. *Br. J. Anaesth.* **84**, 250–253 (2000).
108. Thiel, C. M., Zilles, K. & Fink, G. R. Nicotine modulates reorienting of visuospatial attention and neural activity in human parietal cortex. *Neuropsychopharmacology* **30**, 810–820 (2005).
109. Kosslyn, S. M., Thompson, W. L., Costantini-Ferrando, M. F., Alpert, N. M. & Spiegel, D. Hypnotic visual illusion alters color processing in the Brain. *Am. J. Psychiatry* **157**, 1279–1284 (2000).
A PET study showing the influence hypnotic suggestion (that is, top-down effects) can wield on stimulus-driven neurophysiology (that is, bottom-up effects).
110. Raz, A. in *Cognitive Neuroscience of Attention* (ed. Posner, M. I.) 420–429 (Guilford, New York, 2004).
A brief account of the idea of 'atypical attention' and how it can be used in cognitive neuroscience research to study attention.
111. Raz, A. & Norman, K. L. A social psychologist illuminates cognition. *Behav. Brain Sci.* **27**, 673–674 (2004).
112. George, M. S. *et al*. Transcranial magnetic stimulation. *Neurosurg. Clin. N. Am.* **14**, 283–301 (2003).
113. Dillbeck, M. C. Meditation and flexibility of visual perception and verbal problem solving. *Mem. Cognit.* **10**, 207–215 (1982).
114. Alexander, C. N., Langer, E. J., Newman, R. I., Chandler, H. M. & Davies, J. L. Transcendental meditation, mindfulness, and longevity: an experimental study with the elderly. *J. Pers. Soc. Psychol.* **57**, 950–964 (1989).
115. Wenk-Sormaz, H. Meditation can reduce habitual responding. *Altern. Ther. Health Med.* **11**, 42–58 (2005).
116. Raz, A., Kirsch, I., Pollard, J. & Nitkin-Kaner, Y. Suggestion reduces the Stroop effect. *Psychol. Sci.* **17**, 91–95 (2006).
Proposes that suggestibility is perhaps more important than hypnotic induction and that individuals who are highly suggestible can 'deautomatize' cognitive processing (that is, Stroop interference) in the presence of hypnosis but also in its absence.
117. Besner, D. The myth of ballistic processing: evidence from Stroop's paradigm. *Psychon. Bull. Rev*. **8**, 324–330 (2001).
118. Neely, J. H. & Kahan, T. in *The Nature of Remembering: Essays in Honor of Robert G. Crowder* (eds Roediger, H. L., Nairne, J. S., Neath, I. & Surprenant, A. M.) 69–93 (American Psychological Association, Washington, DC, 2000).
119. Carter, O. L. *et al*. Meditation alters perceptual rivalry in Tibetan Buddhist monks. *Curr. Biol.* **15**, R412–R413 (2005).
Evidence from meditative practices suggesting that attentional training can have profound influences on cognition.
120. Desimone, R. & Duncan, J. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18**, 193–222 (1995).
121. Pessoa, L., Kastner, S. & Ungerleider, L. G. Neuroimaging studies of attention: from modulation of sensory processing to top-down control. *J. Neurosci.* **23**, 3990–3998 (2003).
122. Astafiev, S. V., Shulman, G. L. & Corbetta, M. Visuospatial reorienting signals in the human temporo–parietal junction are independent of response selection. *Eur. J. Neurosci.* **23**, 591–596 (2006).
123. Sapir, A., d'Avossa, G., McAvoy, M., Shulman, G. L. & Corbetta, M. Brain signals for spatial attention predict performance in a motion discrimination task. *Proc. Natl Acad. Sci. USA* **102**, 17810–17815 (2005).
124. Corbetta, M. & Shulman, G. L. Control of goal-directed and stimulus-driven attention in the brain. *Nature Rev. Neurosci.* **3**, 201–215 (2002).
125. Lutz, A., Greischar, L. L., Rawlings, N. B., Ricard, M. & Davidson, R. J. Long-term meditators self-induce high-amplitude γ synchrony during mental practice. *Proc. Natl Acad. Sci. USA* **101**, 16369–16373 (2004).
126. Raz, A. *et al*. Ecological nuances in functional magnetic resonance imaging (fMRI): psychological stressors, posture, and hydrostatics. *Neuroimage* **25**, 1–7 (2005).
127. Robertson, I. H., Mattingley, J. B., Rorden, C. & Driver, J. Phasic alerting of neglect patients overcomes their spatial deficit in visual awareness. *Nature* **395**, 169–172 (1998).
Patients with neglect have long been studied as good models of a deficient orienting system. However, this study shows that the influence of phasic alerting suggests that attentional subtypes can interact, thereby redefining the concept of independence in attentional networks.
128. Corbetta, M., Kincade, M. J., Lewis, C., Snyder, A. Z. & Sapir, A. Neural basis and recovery of spatial attention deficits in spatial neglect. *Nature Neurosci.* **8**, 1603–1610 (2005).
129. Manly, T., Dobler, V. B., Dodds, C. M. & George, M. A. Rightward shift in spatial awareness with declining alertness. *Neuropsychologia* **43**, 1721–1728 (2005).
130. Rueda, R. M., Rothbart, M. K., McCandliss, B. D., Saccomanno, L. & Posner, M. Training, maturation, and genetic influences on the development of executive attention. *Proc. Natl Acad. Sci. USA* **102**,14931–14936 (2005).
131. Klingberg, T. *et al*. Computerized training of working memory in children with ADHD — a randomized, controlled trial. *J. Am. Acad. Child Adolesc. Psychiatry* **44**, 177–186 (2005).
132. Klingberg, T., Forssberg, H. & Westerberg, H. Training of working memory in children with ADHD. *J. Clin. Exp. Neuropsychol.* **24**, 781–791 (2002).
133. Olesen, P. J., Westerberg, H. & Klingberg, T. Increased prefrontal and parietal activity after training of working memory. *Nature Neurosci.* **7**, 75–79 (2004).
134. Parasuraman, R., Greenwood, P. M., Kumar, R. & Fossella, J. Beyond heritability: neurotransmitter genes differentially modulate visuospatial attention and working memory. *Psychol. Sci.* **16**, 200–207 (2005).
A thoughtful account of how a brain theory together with a careful correlation of genotype with phenotype can advance our understanding of attention.
135. Ramel, W., Goldin, P. R., Carmona, P. E. & McQuaid, J. R. The effects of mindfulness meditation on cognitive processes and affect in patients with past depression. *Cognit. Ther. Res.* **28**, 433–455 (2004).
136. Ekman, P., Davidson, R. J., Ricard, M. T. & Wallace, A. B. Buddhist and psychological perspectives on emotions and well-being. *Curr. Dir. Psychol. Sci.* **14**, 59–63 (2005).
137. Landau, S. M., Schumacher, E. H., Garavan, H., Druzgal, T. J. & D'Esposito, M. A functional MRI study of the influence of practice on component processes of working memory. *Neuroimage* **22**, 211–221 (2004).
138. Garavan, H., Kelley, D., Rosen, A., Rao, S. M. & Stein, E. A. Practice-related functional activation changes in a working memory task. *Microsc. Res. Tech.* **51**, 54–63 (2004).
139. Fan, J., Fossella, J., Sommer, T., Wu, Y. & Posner, M. I. Mapping the genetic variation of executive attention onto brain activity. *Proc. Natl Acad. Sci. USA* **100**, 7406–7411 (2003).
Together with the work of Parasuraman *et al*. (see reference 134), these exploratory studies show how genetics could have a role in shaping the biological substrates of attention.
140. Konrad, K. *et al*. Development of attentional networks: an fMRI study with children and adults. *Neuroimage* **28**, 429–439 (2005).
Reference 140 and 141 provide information about the development of attentional networks.
141. Fan, J., Wu, Y., Fossella, J. A. & Posner, M. I. Assessing the heritability of attentional networks. *BMC Neurosci.* **2**, 14 (2001).
142. Parasuraman, R. & Greenwood, P. M. in *Cognitive Neuroscience of Attention* (ed. Posner, M. I.) 245–259 (Guilford, New York, 2004).
143. Diamond, A., Briand, L., Fossella, J. & Gehlbach, L. Genetic and neurochemical modulation of prefrontal cognitive functions in children. *Am. J. Psychiatry* **161**, 125–132 (2004).
144. Egan, M. F. *et al*. Effect of COMT Val108/158 Met genotype on frontal lobe function and risk for schizophrenia. *Proc. Natl Acad. Sci. USA* **98**, 6917–6922 (2001).
145. Greenwood, P. M. & Parasuraman, R. Normal genetic variation, cognition, and aging. *Behav. Cogn. Neurosci. Rev.* **2**, 278–306 (2003).
146. Hariri, A. R. & Weinberger, D. R. Imaging genomics. *Br. Med. Bull.* **65**, 259–270 (2003).
147. Grandy, D. K. & Kruzich, P. J. in *Cognitive Neuroscience of Attention* (ed. Posner, M. I.) 260–268 (Guilford, New York, 2004).
148. Raz, A., Fossella, J. A., McGuiness, P., Zephrani, Z. R. & Posner, M. I. Neural correlates and exploratory genetic associations of attentional and hypnotic phenomena. *Hypnose und Kognition* **2**, 79–92 (2005).
149. Sommer, T., Fossella, J. A., Fan, J. & Posner, M. I. Inhibitory control: cognitive subfunctions, individual differences and variation in dopaminergic genes. *Proc. Hanse Institute* (in the press).
150. Mottaghy, F. M. *et al.* Systems level modeling of a neuronal network subserving intrinsic alertness. *Neuroimage* **29**, 225–233 (2006).

Acknowledgements

We thank M. Posner, R. Parasuraman and I. Robertson for helpful discussions and constructive comments regarding early versions of this manuscript.

Competing interests statement

The authors declare no competing financial interests.

DATABASES

The following terms in this article are linked online to:
Entrez Gene: http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=gene
CHRNA4 | *DRD4*
Access to this links box is available online.