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Research paper

Attention in the heart of intelligence

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A B S T R A C T

Objective: Spearman's notion of general intelligence (*g*) denotes the existence of a general mental ability that contributes to successful performance of diverse cognitive tasks. But, what cognitive processes underlie this *g* factor?

Method/Results: In this paper, I discuss several pieces of evidence that suggest that general intelligence largely relies on a basic capacity to regulate mental activity according to goals and intentions, allowing for the relatively fast and flexible adaptation to changing conditions, a mechanism prominently associated with the executive control of attention.

Conclusion: This body of evidence advocates for training attention as a strategy to promote people's mental capital. Some data to this respect show very exciting results, however, additional research is needed before we determine the nature of most effective interventions.

1. Facets of attention

Aspects of activation, selection and control have been involved in the construct of attention from early to more recent theoretical models [1,2]. We live in a complex environment which provides a vast amount of stimulation. In this complex world, attention serves as the interface between all the stimulation reaching our senses and the more limited set of information we are able to consciously process at a time. In this sense, attention is a selection mechanism that serves to choose a particular source of stimulation for priority processing, and is closely connected to consciousness. On the other hand, attention has been largely linked to the voluntary and effortful control of action, as opposed to well-learned automatic behavior. Very often we do things automatically. For example, we can perform a quite complex motoric act such as running or biking while our attention is focused in a different activity, as for example appreciating the scene or having a conversation with a friend. Automatic actions do not require attention control. However, in certain situations attention is necessary to supervise goal-directed action. These are situations that involve overcoming an automatic course of action and detecting the need to do so. Also, attention is necessary for detecting errors, and controlling behavior in dangerous and novel or unpracticed conditions [3]. Thus, attention mechanisms are also central to the generation of voluntary behavior, which often involves inhibition of automatic response tendencies. Finally, attending also entails an optimal level of activation. Efficiency of attention is greatly affected by conditions in which our level of activation is compromised, such as fatigue or drowsiness (see Fig. 1).

These three broad aspects of attention, activation, selection, and control, can in turn be subdivided in subordinate functions or operations (see Table 1). An important subdivision axis is related to whether the particular function is mostly driven by external stimulation or else relies on endogenous processes such as voluntary intentions or expectations. In the scope of selectivity, attention can be oriented to an object or space automatically because of an abrupt change in stimulation occurring there. This happens, for instance, when somebody waves arms to call our attention or a white sail pops-out in the largely homogeneous bluish background of the sea. On the contrary, attention can also be directed to an object because of its relevance to our current goals. If I search for a friend in a crowd of people and I know that she is wearing a green t-shirt, attention will bias the visual system toward the detection of green objects. These two modes of guiding attention are respectively referred to as exogenous or stimulus-driven (bottom-up) and endogenous or goal-directed (top-down) orienting of attention [4].

Likewise, the alerting state of the individual can be varied endogenously, for example because of a change in motivation (e.g. I am interested in the topic of a talk) which facilitates sustaining attention over longer periods of time. Or else, the level of activation can be varied exogenously because of a sudden change in stimulation (e.g., the sound of an alarm). Very often sustained or tonic attention relies on voluntary processes while phasic preparation is automatic and linked to changes in stimulation.

Finally, the exogenous vs endogenous division can be also applied to control processes. While attention control processes have been conventionally considered voluntary and endogenous by definition [5], some authors argue that certain processes related to executive control such as facilitation of processing due to repetition (i.e. priming and conflict adaptation) can be carried out automatically [6]. Nonetheless, the operations that are usually linked to cognitive control are conscious detection, inhibition, and conflict processing [5,7]. Conscious detection is necessary for voluntarily responding to a target. This is easily

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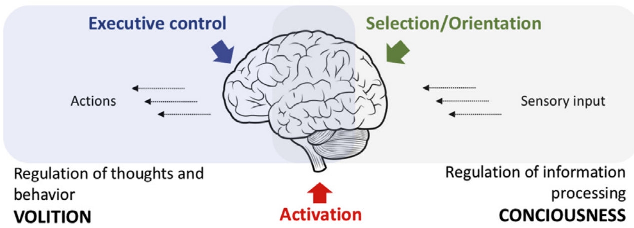

Fig. 1. Attention is a mechanism that regulates the flow of information in the brain.

Table 1
Facets of attention
Attention is related to aspects of activation, selection and control. These facets of attention can be further divided according to whether attentional responses are externally or internally (voluntarily) controlled.

	EXOGENOUS (external control)	ENDOGENOUS (internal/voluntary control)
ACTIVATION	Preparation	Sustained attention / vigilance
SELECTION	Stimulus-driven (bottom-up) attention	Goal-directed (top-down) attention
CONTROL	Automatic tendencies: practiced tasks Priming Sequential effects	Conflict: overcoming dominant responses Error-detection and correction Novel and/or dangerous tasks

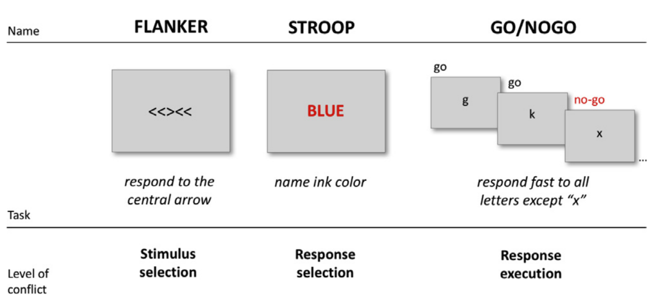

Fig. 2. Classic conflict tasks.

observed in the context of making mistakes. Errors cannot be corrected unless they are detected. In fact, error detection is very often studied as a cognitive control mechanism involved in action regulation [8]. Another way to study executive control in the lab consists of inducing conflict between responses by instructing people to execute a subdominant response while suppressing a dominant tendency. A variety of conflict-inducing tasks have been used to study cognitive control (see Fig. 2). Different tasks vary in the stage of information processing in which interference is induced. For instance, in the flanker task, interference is produced by presenting distracting stimuli that compete with the target at the perceptual level. In the Stroop task, the dominant (word reading) and required (color naming) responses are brought about by the very same stimulus, thus interference is induced at the level of response selection. Finally, in Go/NoGo tasks, the rapid responses to frequent Go stimuli interferes with the need to hold the response to infrequent NoGo stimuli, in which cases control is mostly operating at the level of response execution. In the different types of conflict-inducing tasks, inhibition is necessary to withhold the dominant incorrect response and develop the appropriate one.

In sum, attention can be defined as a multidimensional construct that refers to a state in which we have an optimal level of activation that allows selecting the information we want to prioritize in order to control the course of our actions. Moreover, the attentive state can be primarily driven from external stimulation or be under the voluntary control of the individual.

1.1. Attention and intelligence

The relationship between selective, sustained and executive attention, as well as other executive processes such as working memory, and general intelligence is well documented in the literature. Very often, all these processes are described as *frontal lobe functions*, stressing their contribution to goal-directed control of thoughts and actions. In a seminal review paper published in 2002, Kane and Engle proposed to use an executive attention framework for unifying the different constructs utilized to describe the function of the prefrontal cortex, given the "*unique executive attention role in actively maintaining access to stimulus representations and goals in interference-rich contexts*" [9].

Core aspects of fluid intelligence, such as reasoning and problem-solving are often included in the umbrella of frontal lobe functions. In fact, fluid intelligence highly overlaps with the so-called higher-level executive functions, namely reasoning, problem-solving and planning [10]. Thus, it comes with no surprise that measures of executive attention and working memory are highly correlated with fluid intelligence [11–13]. Researchers using structural equation modeling in order to understand the contribution of different cognitive processes to intelligence and its development, have proposed a hierarchical structural model of intelligence where higher-order reasoning abilities build upon lower-level processes related to cognitive control and speed of processing [13]. Also, studies with children and adults have shown that both the scope and control of attention contribute to individual differences in intelligence, and that the internal control of attention acts in the service of memory processes to influence reasoning skills [12]. Hence, there is evidence that both storage capacity and executive attention contribute significantly to fluid intelligence and complex learning skills [14] both in adulthood and during development.

2. Brain networks

The three general functions of attention just described have been associated with distinct brain networks within Posner's neurocognitive model of attention [15,2]. Alerting has been linked with activation coming from the brain stem arousal system along with frontal and parietal regions related to sustained vigilance.

Regarding selective attention, studies that combine neuroimaging techniques with orienting paradigms in which cues are used to prompt attention to particular locations, have led to the identification of two different brain networks involved in selective attention. The two networks are distinctively activated (1) when focusing attention voluntarily using top-down control mechanisms, or (2) when exogenous and relevant stimuli appear in the environment inducing reorienting of attention according to task demands. In the first case, performance of top-down orienting tasks has been associated with the activation of a bilateral dorsal-frontoparietal network that involves the intra-parietal sulcus (IPS), the superior parietal lobule (SPL) and the frontal eye fields (FEF). In the second case, detection of infrequent or miscued but salient targets has been related to increased activation in a right-lateralized network of ventral fronto-parietal structures including the temporo-parietal junction (TPJ) and inferior frontal cortex [16]. Analyses of spontaneous fluctuations in blood oxygenation (BOLD signal) at rest provide a measure of functional connectivity, because regions that are functionally connected show correlated fluctuations in the BOLD signal over time, even at rest. Studies using this method have revealed that the two attention systems are clearly segregated and exhibit only a small overlapping region in the prefrontal cortex [17]. Despite their anatomical and functional dissociation, the dorsal and ventral systems dynamically interact to ensure a flexible and efficient control of attention [18]. Thus, when a person is engaged in a task, structures in the dorsal system appear to send top-down signals that not only modulate the activation of sensory systems according to current goals [19], but also suppress the activation of the ventral system to restrict its activation to stimuli that are relevant [16]. Thus, when salient cues carrying out relevant information for the task at hand are presented, the right TPJ exhibits a significant increase of activation that is associated with improved performance of the task [20].

With respect to attention control, also called *executive attention*, numerous neuroimaging studies have shown that diverse conflict tasks, as those presented in Fig. 2, show a common node of activation in the anterior cingulate cortex (ACC) together with other regions of the lateral prefrontal cortex [21,22]. This led Botvinick and colleagues to propose the conflict monitoring account, which suggest that the ACC is involved in conflict detection and monitoring, while lateral frontal areas are in charge of implementing processes (e.g., inhibitory control) aimed at selecting appropriate responses [23]. The structure of connections of the ACC with other brain regions makes it a good candidate for executive control. Different parts of the ACC are well connected to a variety of other brain regions, including limbic structures as well as parietal and frontal areas. Recent studies have examined the connectivity of the executive network at rest and have shown that two functionally different but complementary circuits are engaged when implementing cognitive control: the fronto-parietal and the cingulo-opercular networks [24]. The fronto-parietal network is related to processing of cognitive control signals that potentially initiate response adjustments on a trial-by-trial basis. This network includes the dorsolateral prefrontal cortex (dlPFC), inferior parietal lobule (IPL), dorsal frontal cortex (dFC), intra-parietal sulcus (IPS), precuneus, and middle cingulate cortex (mCC). On the other hand, the cingulo-opercular network is involved in maintaining a stable task set during performance; that is, representing the goal of the individual in the context of the task and the corresponding stimulus-to-response mapping along many trials [25]. This network includes the anterior prefrontal cortex (aPFC), anterior insula/frontal operculum (aI/fO), dorsal anterior cingulate cortex/medial superior frontal cortex (dACC/msFC) and the thalamus (see Fig. 3).

In relation to intelligence, cognitive neuroscience theories propose that individual differences in general intelligence (Spearman's g) originates from the function of localized brain regions, which show a remarkable overlap with attention-related networks. In diverse imaging studies, John Duncan and colleagues showed that the type of tasks commonly used to measure the “g factor” activate a specific frontal network involved in the control of attention and behavior, including the mid-dorsolateral, mid-ventrolateral and dorsal ACC [26,27]. Likewise, Jung and Haier [28] reviewed a large number of neuroimaging studies aiming at understanding the brain basis of human intelligence and proposed the Parieto-Frontal Integration Theory of intelligence (P-FIT). According to the P-FIT model, variations in general intelligence are accounted for on the basis of the function of a broadly distributed network of parietal and frontal areas, with main nodes in the dlPFC, inferior and superior parietal lobe, and ACC. This network-based theory of intelligence emphasizes the integration of information between frontal and parietal cortex as the key feature of intelligent behavior. The efficient flow of information is facilitated by the presence of well myelinated white matter fibers among those regions but can also be observed at the level of functional network dynamics [29]. As I will discuss in the following section, the efficient processing of information within the attention networks appears to be a brain marker of intelligence.

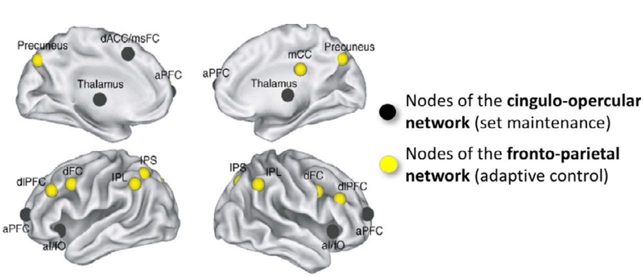

Fig. 3. Nodes of the cingulo-opercular and fronto-parietal networks related to executive attention. Adapted and reproduced with permission from [25].

3. Attention and the efficient processing of information

As defined in the previous paragraph, the primary role of attention is to regulate the flow of information in the mental working space of individuals. We experience a limited amount of all the information reaching our senses. A great deal of this information is implicitly processed and we are not even aware of it. This is because the unconscious processing of information is much cheaper in terms of cognitive resources than the attentive, conscious processing of information. Think about walking up the stairs while having an important conversation with your boss. The conscious working space of your mind is occupied with listening and arguing, little or no resources are devoted to controlling the visual information of the steps and the (quite complex) sequence of motor actions that are taking place to go up the stairs. The content of the mind, at least the part of the mind involved in making decisions and planning behavior according to internal goals, is shaped by the information we experience at any given time. Attention is the mental mechanism that regulates the flow of information within this mental working space. In William James' words “*My experience is what I agree to attend to. Only those items that I notice shape my mind – without selective interest […] the consciousness of every creature would be a gray chaotic indiscriminateness, impossible for us even to conceive*” (James, 1890, pp. 402–3). Relevant classical models of attention have emphasized its role in filtering out irrelevant information [30], and administering cognitive resources among relevant tasks [31], in order to maximize the efficient processing of information in and out the mental working space of individuals (see Fig. 1).

A property of our cognitive system is its proneness toward generating courses of actions that are low-demanding in terms of executive control resources. This economizes the use of cognitive resources and maximizes its distribution toward the more attention-demanding actions or trains of thoughts [3]. As an example, in the first stages of learning to ride a bike, all cognitive resources are devoted to controlling the sequence of actions needed to keep the bike straight and moving. Once the very many motor control schema have been generated and automatized, cognitive resources are freed and can be used for other purposes while riding the bike. The process of learning to ride a bike is a very complex one that involves the coordination of lots of muscles and actions, hence it can take days or weeks of intensive practice to complete automatization. However, learning processes governed by this principle of economization of resources (automatization) are very much entrenched in our cognitive system and can be observed even after just one trial. It is well known that performing a simple task such as naming a picture is facilitated when the same picture was named before (i.e., perceptual priming) or even when the picture of an associated element was named before (e.g., the picture of a lion, and then the picture of a tiger; i.e., semantic priming). Likewise, if I just perform a difficult task, for example a task involving some degree of conflict (i.e., an incongruent Stroop trial, as in Fig. 2), resolving a similar situation is facilitated, as compared to when a difficult task follows an easy one (i.e., a trial in which color and name are congruent). These are named sequential effects and have been much studied since Gratton and colleagues described them for the first time [32]. All these mechanisms are examples of how our brain optimizes the use of cognitive resources. Also, these robust cognitive effects are consistent with Hebbian learning principles, according to which repeated co-activation during everyday activity lead to the establishment of greater synaptic efficiencies between the co-activated regions [33]. However, as much automatization facilitates fast responses and economizes resources, an excess of it may lead to inflexible behavior. Therefore, flexible adaptation to rules and goals requires regulation of automatic response tendencies. Hence, optimal performance demands a fine balance between the activation of automatic pathways and control processes that regulate them.

Very modern neuroimaging methods have helped to elucidate how the brain organizes the processing of information in order to economize resources [34]. The brain is a complex system where segregated regions form a complex network that continually processes and integrates information at various temporal and spatial scales. The organization of functional brain networks can be inferred from temporal correlations between variations in activation levels in different regions of the brain obtained with neuroimaging technology in the absence of cognitive demands (i.e., with resting state fMRI, EEG, or MEG data). The analysis of the brain's functional connectivity patterns in the emerging field of network neuroscience suggests that, searching for the balance between minimizing costs and allowing flexible and adaptive courses of actions, the brain organizes the processing of information into specialized local modules and interconnections between them [35]. This creates a so-called *small-world* architecture characterized by two information processing spaces, one local and one global, that are dynamically interconnected. Local modules are composed of densely interconnected cortical regions or nodes. These modules perform specific cognitive operations, and hence form the basis for regional functional specialization of the brain. The spatial proximity of nodes within each module increases the speed of signal transmission and enhances the local efficiency of information processing, thus minimizing mental cost. However, in order to maximize flexibility and adaptation, the system requires an architecture of connections between modules that enables the dynamic integration and coordination of information across the network. Therefore, efficiency of information processing within the network is achieved by balancing the competition between decreasing the cost for local specialization and increasing the connection distance between modules in order to facilitate the global transfer of information [35]. Using the computational approach of graph theory, the efficiency of information processing of a given region of the brain (*nodal efficiency*) or the brain as a whole (*global efficiency*) is characterized by computing two indices based on functional connectivity data obtained with MRI [36]. On the one hand, nodal efficiency provides an index of the degree a particular region of the brain is closely connected to the rest of the network by means of short and functionally strong connections. As a counterpart, global efficiency is calculated as the average of nodal efficiency values of all nodes in the network, thus providing an index of the extent to which an individual presents a pattern of efficient (short and strong) connectivity across the whole brain.

As a new skill is learned, performance changes from being challenging and slow to being fast and automatic. This suggests that repetitive activation of a module with increased practice enhances the flow of information within the module. This can be accomplished by either changing the architecture of node connections within the module or boosting the easiness with which the module reaches a state of optimal activation (excitability of the circuit). Bassett and colleagues have shown that the modular structure underlying learning of a simple motor skill changes dynamically with repetitive practice [37]. At early stages of learning, the allegiance of nodes to modules involved in the task being learned is more flexible, whereas nodal flexibility decreases with practice. Interestingly, nodal flexibility at earlier stages of the process is predictive of learning success. An important consequence of this is that greater initial nodal flexibility confers adaptability to the system by reducing constraints on the modular organization. It is possible that attention control at early stages of learning is required to optimize coordination between modules and optimizing the establishment of more stable allegiance of nodes to modules.

3.1. Efficiency of the executive attention network and intelligence

Examining the intrinsic functional organization of the brain and associated efficiency of information processing provides a method for understanding the neural basis of individual differences in intelligence. In a seminal study facing this question, van der Heuvel and colleagues showed a strong negative association between the average path length of functional connections across the whole brain and the level of intelligence, with more pronounced effects at the medial prefrontal cortex, inferior parietal and posterior cingulate/precuneus [38]. Because shortest paths allow faster transmission of information, this finding suggests that intelligence is related to how efficiently the brain of an individual integrates information flowing across the brain, particularly between frontal and parietal regions. The association between *small-world* functional organization of the brain, characterized by short path length and high clustering of functional connections, has been corroborated using high-density EEG [39]. Again, measuring neural electrical signals on the scalp, the connectivity circuit showing the strongest correlations with intelligence was the one linking activity associated with ACC and bilateral parietal cortices, a circuit that nicely overlaps with both the P-FIT theory and regions within the Dosenbach's dual executive control networks.

In a recent study carried out by Hilger and colleagues (2017) with a larger number of subjects, they found that general intelligence was associated with nodal efficiency in three regions of the brain, the dorsal division of the ACC, the anterior insula (AI), and the temporo-parietal junction (TPJ) of the left hemisphere [40]. The first two regions showed a positive association with intelligence, whereas the last one was negatively associated (see Fig. 4). As explained before, nodal efficiency is a measure of efficient processing of information of a particular region of the brain. Therefore, this result gives a central role to two regions of the cingulo-opercular network, dACC and AI, when it comes to explaining individual differences in brain functional organization underlying intelligence. Remarkably, the global efficiency index was not related to intelligence in this study suggesting that it is the processing of information carried out by those particular brain regions and their specific functional contributions what influences global intelligence.

But, what is special about these regions? In addition to indices of nodal and global efficiency, network analysis of brain connectivity also provides information about so-called network hubs. These are nodes that present a high degree of interactions with other nodes and consequently occupy a central position in the network [41]. In the study by Hilger and colleagues, it was found that dACC and AI, the two regions which nodal efficiency was positively related to intelligence, can be considered hubs given their high degree of centrality (high number of other nodes of the brain connecting with them) [40]. Taken together, these data indicate that the main property contributing to individual differences in general intelligence is the integration of information within regions of the brain that enable people to regulate attention and select appropriate responses according to current stimulation and goals.

4. Co-evolution of executive attention and intelligence

The exogenous vs endogenous subdivision of attention processes is very relevant from a phylogenetic point of view. Humans share with other species many cognitive capacities, such as sensory processing in different modalities, associative learning and memory, and even sensory-motor learning of the trial and error type. These capacities are basic and automatic to a large extent because they require none or a low level of voluntary control. Exogenous or reactive attention is among these basic capacities. However, humans exceed other species in their capacity for endogenous control of attention and behavior. Humans possess unrivaled capacity to control attention in goal-directed tasks, which allows to flexibly configure the flow of information processing in order to adapt to changing conditions.

A landmark of the evolution of the genre *homo* about 2 million years ago is the remarkable increase in brain volume compared to hominids ancestors who lived in the Pliocene and early Pleistocene (i.e., Australopithecus and Paranthropus especies). Homo species surpass encephalic capacity of 600 cm^3, which has increased up to about 1600–1700 cm^3 in later evolving species Homo Sapiens and Homo Neanderthalensis [42]. However, the growth of the cranial capacity was not equally distributed along the different regions of the brain. Despite

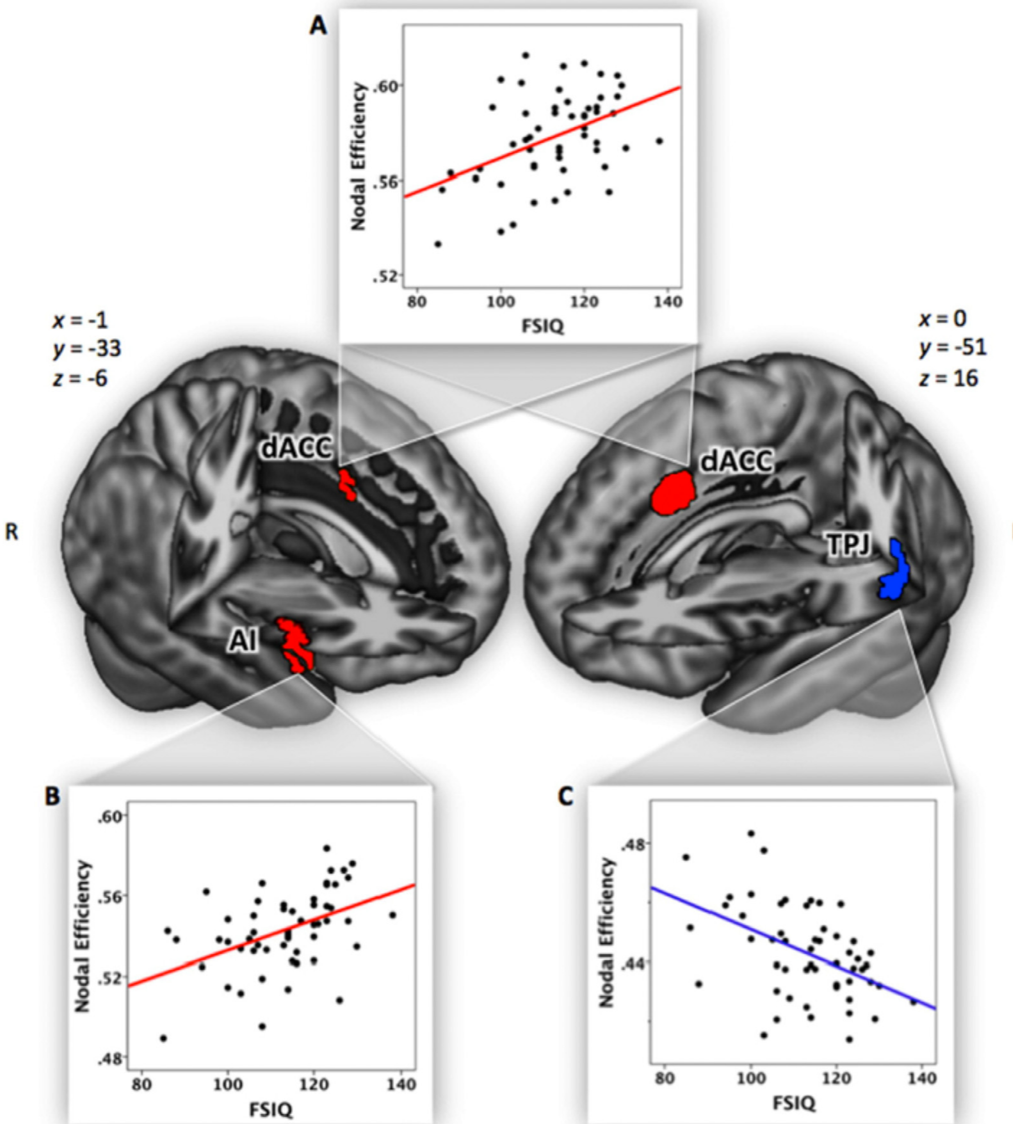

Fig. 4. Regions of the brain which efficiency of information processing is associated with fluid intelligence. Reproduced with permission from [40].

their similar, or even some larger cranial capacity of Homo Neanderthalensis compared to us, an important difference between the two species is that whereas the greater encephalization in Neanderthals is observed in occipital areas, in Homo Sapiens it is much larger in the parietal and frontal regions [43]. These features are observable when comparing cranial fossils of Neanderthals to Homo Sapiens' skulls, but comparing the structure of the brain tissue between these species is impossible.

A possible way to understand the expansion of the brain along evolution and its relationship to improvement in cognitive skills is to compare human brains to those of other primates. Using a quite ingenious analysis of brain structure with MRI, a recent study has provided evidence suggesting that regions of the brain that show the greater expansion during evolution are related to improved intellectual function. Fjell and colleagues compared aerial expansion of different regions of the brain between macaque monkeys and humans (i.e., phylogenetic expansion), as well as between human children and adults (i.e., ontogenetic expansion), by computing the cortical surface area of brains using MRI images [44]. They found that high-expanding areas of the brain are substantially overlapping in both evolution and development (see Fig. 5a). In addition, they were able to compute the correlation between aerial expansion of the cortex and fluid and verbal IQ in the human sample. Interestingly, when mapping together both types of data, they found that several regions of the frontal cortex, particularly the ACC, showed a high expansion in both development and evolution. Moreover, they showed that cortical regions that were high expanding in both phylogenetic and ontogenetic processes, specifically a large portion of the ACC, were in turn related to individual differences in fluid reasoning among humans (Fig. 5b). This suggests that the cortical extension of the ACC, an important node of the executive attention network, has a central role in the development of high cognitive function along both evolution and development.

Cytoarchitectonic studies also support the central role of ACC in human evolution. It has been reported that a type of projection neurons, called von Economo neurons, are specific to humans and great apes, being particularly abundant in humans [45]. Further, this type of neuron is present in exceptionally large numbers in the ACC, where their volume is correlated with brain volume across primates, and the anterior insula [45,46]. This indicates that the ACC played a uniquely important role in hominid brain evolution. Moreover, the uneven

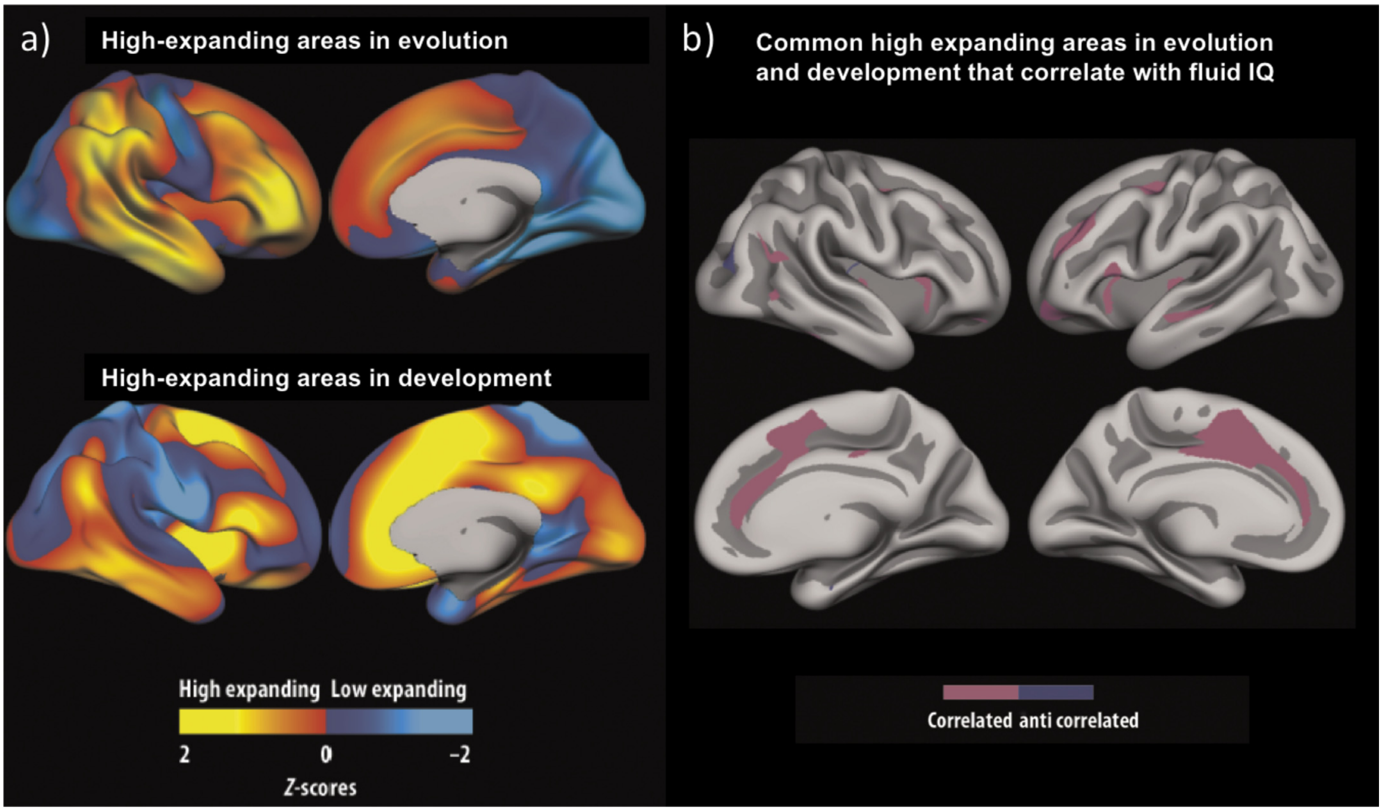

Fig. 5. High-expanding cortical regions in evolution and human development in relation to individual differences in fluid intelligence. Adapted and reproduced with permission from [44].

distribution of this type of neurons in ACC and AI suggests that the different control systems involved in set maintenance and adaptive control might have followed separate evolutionary trajectories. The cytoarchitectural distinctiveness of the human ACC indicates that the set maintenance system is likely to have evolved more recently than the adaptive control system, which would contribute to explain the greater reliance on stable set maintenance in goal-directed behavior that is characteristic of humans [25].

In sum, all these different pieces of evidence are consistent with the idea of human's intelligent behavior greatly relying on the capacity to regulate attention and behavior according to goals and intentions.

5. Do benefits of attention training transfer to intelligence?

In the last decade, there has been growing interest in studying benefits of training at the level of cognitive performance and brain plasticity. It has been suggested that the nature of training exercises may produce either a specific impact on the efficiency of the targeted brain network or a more general influence affecting the dynamical state of the brain [47]. Training programs often consist of computerized exercises that engage the skills they aim to train in increased levels of difficulty. Several studies using these so-called process-based training interventions have shown efficacy gains in selective attention [48], attentional flexibility [49], working memory [50], and inhibitory control tasks [51] following training.

However, the transfer of training benefits to non-trained tasks (i.e. far-transfer) has been a matter of intense debate. Although research yields mix results, a considerable number of previous attention and working memory training studies have been shown to produce gains in fluid intelligence (*fIQ*) in young children [52,53], older children [50,54], and adults [55,49]. Despite all this evidence, other studies have failed to find significant transfer effects of executive processes to fluid intelligence [56,57] and argue that transfer to intelligence may need more sustained training, or that training might not impact intelligence at the construct level but benefit more basic processes taxed by training activities.

Because of high cost of sustained interventions, very often training studies are limited to just a few sessions of training, which rarely go beyond 10 or 12 sessions. This is an important limitation of many studies published so far. However, many training studies have tested whether post-training improvements are related to training-induced brain plasticity using neuroimaging techniques. Using brain measures may provide a more sensitive test of training effects for short interventions because observable effects at the behavior level necessarily reflect changes in underlying brain processes. Reported findings show that cognitive training influences brain plasticity at different levels. Using EEG, we studied training-induced changes in the efficiency of the executive attention networks in a sample of preschool-age children [58,53]. Results revealed that attention training produces a reduction of latency and a shift of topography of conflict-related activations, suggesting a more advanced pattern of activation after training. In a more recent study, we have shown that training executive attention accompanied by metacognitive scaffolding, provided by an adult, boosts transfer of training to fluid intelligence in 5-year-old children, and that the fluid IQ gain following training is predicted by changes in conflict-related brain activation in the frontal midline [59].

Changes in activation of pre-frontal (middle frontal gyrus) and parietal (intra-parietal, and inferior parietal) regions has also been reported after working memory training [60]. In addition, different studies have shown that several sessions of training with a working memory program result in increased functional connectivity at rest within the fronto-parietal network [61,62]. Moreover, it has been reported that training induces changes in the binding potential of dopamine D1 receptors in the parietal and prefrontal cortices [63]. Thus, interventions aimed at increasing experience with particular cognitive processes produce changes in a variety of neural mechanisms, which very likely underlie gains in competency observed at the behavioral and cognitive levels.

On a different approach to training, interventions involving groups of contemplative practices, such as meditation, appear to produce brain state changes by influencing the operations of different brain networks. Meditation is a form of mental training that requires the voluntary engagement of executive functions in order to achieve a non-judgmental attention to present-moment experiences [64]. Several studies have shown that meditation training and expertise result in improvements in behavioral performance of tasks that induce conflict monitoring [65,66], allocation of attentional resources [67] increased activation of the ACC [68] and plasticity of white matter [69]. According to Posner and colleagues, white matter changes might be the underlying mechanism that promotes the improvement of communication efficiency between the ACC and other brain areas, contributing to a change in the state of brain dynamics [70]. However, the impact of meditation training is by no means well established in the literature because lack of effects or weak effects of this type of intervention on attention and other behaviors involving self-regulation have been also reported (see [71]). Hence, more research is needed before we can make conclusive statements on this approach to training.

6. Concluding remarks

Spearman's notion of general intelligence emerges from the finding of universal positive correlations between performance of tests of multiple cognitive domains, which was first described by Spearman at the dawn of the 20th century [72]. In this paper, I have presented evidence from diverse perspectives that converges in placing the endogenous regulation of attention at the heart of intelligent behavior. Several pieces of data suggest that general intelligence largely relies on a basic capacity to regulate mental activity according to goals and intentions, allowing for the relatively fast and flexible adaptation to changing conditions, a mechanism prominently associated with the executive control of attention. Firstly, brain imaging studies have shown that across sensory domains, the type of tasks commonly used to measure the "g factor" activate a specific frontal network involved in the control of attention and behavior. Secondly, processing efficiency of nodes within the attention network are associated with individual differences in intelligence. Finally, the expansion of the cortical surface of the anterior cingulate cortex, a central node of the executive attention network, in both phylogeny and ontogeny seem to have played a key role in the evolution of human intelligence. In both evolution and development, the attention-based regulation of thoughts, emotions and behavior in pursuit of one's own or shared goals is a landmark of progress. The various pieces of data presented here point to this capacity as an important part of general intelligence. In fact, self-regulation appears to be a strong predictor of many aspects of an individual's life, as school learning and socio-emotional competence in childhood and adolescence [73], as well as life outcomes including health, wealth and professional success [74].

Training studies help understanding whether and to what extent we can impact the efficiency of brain networks with cognitive interventions. Data have been reported that show the potential of modifying brain systems in order to improve self-regulatory processes. Also, there is some evidence of the transfer of training to fluid intelligence. Although more studies are needed to replicate and validate these findings, the potential of training for both education and prevention/intervention in psychopathology is promising [75]. Evidence to date allows a certain degree of optimism about the possibility of improving people's general cognitive skills by means of education.

Conflicts of interest

I declare no conflict of interest with the information provided in this paper.

Ethical Statement

Relevant ethical issues for the research discussed in this paper should be found at referred citations (see references).

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