THREE ANTI-CORRELATED NEURONAL NETWORKS MANAGING BRAIN ACTIVITY – REVIEW

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ABSTRACT

In order to understand how the brain operates we should take into account it's component which consume most of the energy, which is spontaneous neuronal activity. Imaging techniques like resting state functional connectivity MRI and Independent Component Analysis technique arrrived at the conclusion that there are a couple of neuronal networks activated in tasks implying goal-oriented activity, and include the systems named "dorsal and ventral atention networks". These networks are anti-corrrelated with another network comprising regions which are deactivated during these tasks, and are involved in the self-referential activity. The last ones are named Default network and it's abnormalities are associated with depressive disorders, schizophrenia, Alzheimer disease and autism. Various studies revealed that the "attention networks" are responsive to specific cognitive trainings using working memory and inhibitory control tasks, both in children and adults, and can be used as an effective treatment for some mental disease or for optimizing healthy people mental performance.

Key words: resting state brain activity, brain networks, cognitive training

"DEFAULT NETWORK" OR THE BRAIN ON AUTOMATIC PILOT

In resting state the human brain – although represents only 2% of the total body mass – consumes 20% of it's energy. Most of this energy is used for supporting the communication between neurons. Nevertheless, the risings in neuronal metabolic activity induced by a mental task are very small – bellow 5% – by comparison with the huge energy consume from the resting state. Therefore, most of the data we have about brain's functions comes from the study of only a minor component from it's total activity. In order to understand how the brain operates we should take into account it's component which consume most of the energy – spontaneous neuronal activity (1). Imaging studies from late 90s and early 2000 have revealed that when subjects lay down relaxed, doing nothing, the brain has spontaneous fluctuations between a state named "introspective" and one named "extrospective". Every time the subjects of a study are instructed to relax and try not to engage in any mental activity (a must for establishing the baseline condition for an imaging study), automatic processes occured which are called "introspectives". In the "introspective state" the brain generates a self-oriented thinking characterized by episodic elements (autobiographics), spontaneous images generation, planning and simulation of future activities, scenarios to solve possible future problems. In this state there are activated the following areas and structures: posterior cingulate cortex/retrosplenial cortex (BA 29, 30, 23, 31), medial prefrontal cortex (BA 10), paracingulate gyrus (BA 9, 8, 32), rostral anterior cingulate cortex (BA 32), subgenual cingulate cortex (BA 25), inferior frontal cortex (BA 47), angular gyrus (BA 39), inferior temporal cortex (BA 21), temporal pole (BA 38) and parahippocampal gyrus (BA 36)(2, 3, 4, 5, 6). In "introspective state" there were recorded low frequency spontaneous neuronal fluctuations (bellow 0.1 Hz), their frequency measured by EEG correlating with the fluctuations recorded through BOLD signal by fMRI, covering extended

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areas of the brain, which has been interpreted as part of a network (5). One of the most detailed studies trying to indentify various brain networks is the study of Mantini et al. (7). Using the technique called resting state functional connectivity MRI (re-fcMRI) they identifyed 6 major networks, named R1, R2, R3, R4, R5 and R6. The R1 network coresponds to some parts of "introspective network" and comprises: inferior parietal lobule (BA40), precuneus (BA 31), superior frontal gyrus/medial frontal gyrus (mostly dorsomedial and medial prefrontal areas). This network also includes the hippocampus, suggesting a role for this "introspective network" in learning and memory. Nevertheless, the connectivity with hippocampus – during memories formation – is wider, including the orbitofrontal part of the R6 network, suggesting that both networks fulfill the role of encoding the information into memory (8). In addition, some other studies have shown that gamma activity from "introspective network" R6 is influenced by theta activity from hippocampus. The coordination between neocortical gamma oscillations and theta oscillations from hippocampus probably represents a mechanism that allows information comprised in vast neocortical neuronal assemblies to be transferred to associative networks in hippocampus (9).

Fox et al. (6) arrrived at the conclusion that there are a couple of neuronal networks activated in tasks implying goal-oriented activity, which include the systems named "dorsal and ventral atention networks"; these networks are anti-corrrelated with another network comprising regions which are deactivated during these tasks, involved in self-referential activity. This network has a higher activity during relaxation, when we are not provoqued by anything from the sorrounding environment, and for this reason it was named the "Default network" – representing the automatic, spontaneous brain activity.

THE FUNCTIONS OF DEFAULT NETWORK – VIRTUAL REALITY

In the nervous system, testing of posibilities and expectancies represents the key of probing and revision of cognitive representations, while the plasticity of predictive systems allows trial and error based learning (10). Brain is esentially a prediction machine which creates virtual future states, and it's main function is to generate expectancies regarding forthcoming events and possible outcomes of the actions. The prefrontal cortex has the leading role in generating this virtual world, by manipulating the internal representations, independent to present environment. It has the abillity to enhance the signals which guide information, selectively activating and inhibiting specific representations and neuronal pathways in various parts of the brain, playing rather a modulatory role. The information is stored in posterior areas of the brain – temporal, parietal and occipital, hence the functions of prefrontal cortex concern actively maintainance and integration of information for encoding and recalling (11). PET and fMRI studies have revealed that medial frontal cortex (BA 10, 32) participates in processing representations coupled with episodic, autobiographic (narrative) thinking, especially emotional valenced (2). This area is functionally connected with medial parietal area and posterior cingulate cortex (BA 30, 31, 7), which are also involved in recalling emotionally laden episodic information (4). As emotionally laden are the stimuli in the initially encoding process, as the further activation of the amygdala is in recalling these stimuli, this plus of activation being a waranty for a more detailed and efficient recalling (12).

This mechanism of simulation/anticipation of behavior allows that perceptive activity generated inside it to serve as a reality for a new behavior, coupling in "causal chains" simulated perceptions and simulated actions. By simulating interactions with environment, an organism can assess not only a single action but an entire course of actions, putting them on a virtual test, before the real one, posibly more dangerous (13). "Default network" comprises two distinct subsystems – one which provide information from memory and one which participates in self-relevant mental simulations. It's adaptive functions is a sort of "simulator" running past experiences in order to explore and anticipate scenarios and various social and personal relevant events (14). The simulation of future actions, the process of adopting other person perspective, and navigation in a virtual space, all represent forms of mental construction of alternative visual scene. Simulation of future events requires a system which flexibly recombines the details of past events, episodic memory providing the construction of future events through extraction and recombination of stored data used in simulation of a new event. The system which called Default network has the main function of generation/simulation alternative perspective/reality, the temporal dimension (past/present) being irrelevant (15).

Recent studies concluded that ability to mentally represent the personal future goes "hand in hand" with the ability to represent the past. Thus, episodic memory can be seen as the ability to represent ourselves, both in the past and in the future. Many evidence from clinical psyhology, developmental psyhology and neuropsyhology are congruent with this hypothesis. Specifically, depresive pacients, little children and amnezic patients are unable to remember in details their past, but are equally unable to generate detailed imagines about the future (16). Memory can be seen as an instrument used by the "prospective brain" to generate simulations of posible future events, and also to generate alternatives to what was already happened – so called "counterfactual scenarios"(15, 17). Counterfactual scenarios represent an important part of the daily life. They are based on autobiographic memory and launch alternative hypothesis to the events already happend (i.e. "what would happen if in situation "Z" I take decision "X" instead of decision "Y" ?")(17). A component related with the so-called „future oriented thinking" is one's ability to imagine himself/herself as a participant in a future event, a process which initiates the operations of structuring the behavior. Many of the daily thinking operations rely on the ability to see ourselves as participants on future actions, this ability being named "episodic future-oriented thinking" (16). Situations which presume the planning of activities which will take place in distant future are based on what is called in some experimental paradigms "prospective memory" (18). "Prospective memory" helps us to not forget the final goal during the process of executing various intermediate actions, some of them not directly related with that goal. It is manifesting in complex or ambiguous situations, when many actions are possible and we must decide to implement one of our intentions and to start a goal-oriented behavior (19).

As you can see, various paradigms study the same aspects, with a common anatomical base, only named differently. Imaging studies have shown that in "prospective memory" tasks are involved medial frontopolar area (BA 10), dorsal anterior cingulate cortex (BA 32), premotor/supplemental motor area (BA 6, 8), posterior cingulate cortex (BA 23, 31) and right medial parietal cortex (BA 7) (19, 20, 21). More detailed, PET and fMRI studies pointed that processes of both recalling the past and imagine the future are associated with activity of a system comprising medial temporal area (hippocampus), retrosplenial cortex and precuneus (BA 29, 31, 7), lateral parietal cortex and medial prefrontal/anterior cingulate cortex (BA 10/32) (15). In addition, a set of regions – known as being involved in behavior simulation – are more activated during prospective memory tasks (pre-supplementary motor area – BA8, premotor cortex – BA 6, medial posterior parietal cortex – BA 7, and posterior cerebellum)(specific for motor programing), and another set is equally activated in prospective memory and autobiographic recalling (medial prefrontal cortex – BA 10, posterior cingulate – BA 23, 31, parahippocampal gyrus and occipital cortex – BA 17, 19)(16, 22). The second set is used also in spatial memory task when subject must represent himself in a visuo-spatial context (16). This set lacks the component of motor programing and deals only with the components of temporal and contextual planing (22). So, the ability to mentally represent a future event is based on action simulations and visuo-spatial representations of the context (16).

As I mentioned above, Default network covered a large part of the brain, connecting medial prefrontal region with medial posterior regions. Various studies have revealed that medial prefrontal region (BA 10, 32) is activated whenever we think about our affective states (the rostral part), and also about others' states (the dorsal paracingulate). It is also activated when paying attention to reactivated affective experiences, regardless of valence (positive or negative), when we think about others' beliefs and intentions, in solving moral dilemma based on simulation of many alternatives in order to evaluate them (14, 23, 24). The rostral medial prefrontal (BA 9 – inferior, 10 and 32) is involved in introspection, in monitoring affective state, in making judgements about our own physical and personality traits, but also in making judgements about other people – unfamiliar (the superior part) or familiar (the inferior part), in representing other person's perspective ("mentalization"), in determining the causality of his/her behavior ("attribution"), all these operations being realized through the conections with posterior cingulate area, medial temporo-parietal junction and superior temporal sulcus (25; 26).

Through these circuits a permanent inner rehersal or simulation of behavioral sequences is realized in order to optimize them, in the same time with the evaluation of the rewarding or aversive nature of their possible outputs (2, 3, 6). All these abilities have in common processes of mental simulation used for imagine events beyond immediate reality. The medial posterior cortex – an important part of the Default network – is the brain's area having the highest metabolic activity and the highest resting state activity (3). In resting state, the medial posterior cortex area (including the posterior cingulate cortex) consumes 40% more glucose than the hemispheric average (27). The medial posterior cortex is comprised of posterior cingulate cortex (BA 23a, b and c), retrosplenial cortex (BA 29 and 30), medial parietal (BA 7) and precuneus (BA 31). Anatomical studies have demonstrated that retrosplenial cortex (BA 29, 30) is connected with dorsomedial prefrontal and medial frontal, with ventromedial prefrontal, anterior cingulate cortex (BA 24), basolateral amygdala and ventral caudate nucleus, building a network involved in emotional processing (27). These areas are deactivated during REM and slow-wave sleep, in hypnosis, in vegetative state or during general anesthesia, and are the first activated when a patient comes out of the coma (27, 28). A rising in activity of these areas is recorded when a person is instructed to describe his/her own personality traits and physical appearances, and a drop of activity is recorded when doing the same operations about other people (27, 28). Also, the retrosplenial cortex is activated when we remember autobiographic events (27).

THE ROLE OF EXPERIENCE IN BUILDING THE DEFAULT NETWORK

Studies revealed that Default network is activated when people with strong political knowledge are asked to make judgements regarding various political issues. By the contrary, when are asked to do the same thing novice people use the same brain networks as they try to solve a new problem or an intelligence test (29). Similary, people that make judgements about fictious characters described either being similar sociopolitical with them or diferent, activated Default network in similar condition and not in disimilar condition. These data confirm implication of Default network in what is sometime called “Self”. Although not completely proved, it is possible that Default network be the root of some moral emotions like proud, shame and guilt (14). The rostral medial prefrontal (BA 10, 32) is involved also in evaluating our own personality and physical traits (25) and a common element in processes implemented by Default network is thinking about complex interactions between people, perceived as being socials, interactives and emotives in a similar way with ourselves (14). The involvement of Default network in processing cultural information and familiarity with ourselves, suggests the impact of learning in building this network – Default network could be seen as “the store of long-term memory”, especially of socially valenced information. It is known that Default network has a developmental trajectory, interhemispheric connectivity being strong at 6 years, but not the anterior-posterior connectivity between parietal/posterior cingulate and medial prefrontal areas, which achieves the adult level only at 21 years, suggesting an important role of life experience in shaping this network. In addition, early life stressors could be the cause of some abnormalities in development of the network, probably impacting neurotrophic factors, and thus creating a predisposition toward depressive disorders (30, 31). Studies using Diffusion Spectrum Imaging technique (DSI) by University of Lausanne, Indiana University, Cambridge University and Harvard Medical School, revealed the existence of a “structural core” of the brain, comprising various posterior medial and lateral areas: middle and posterior cingulate cortex, retrosplenial cortex, precuneus, cuneus, primary motor cortex, inferior parietal lobule and posterior parietal. This core has the highest inter-connectivity from the entire brain and acts as a single integrative system wich coordinates the processes from both hemispheres. It is strongly connected with medial frontal regions – caudal and rostral anterior cingulate, medial orbitofrontal cortex, but also with temporal regions (superior and middle temporal gyrus, and superior temporal sulcus) and occipital regions, all parts of the “Default network”. All these regions – both the core and it’s connections – play the role of “hubs” or connecting nodes for various brain networks. There are 6 modules identified, containing 13 provincial hubs and 12 connectors hubs. 9 of the connectors hubs form the core of the brain situated on the axis connecting cuneus, precuneus, posterior cingulate, medial and lateral parietal cortex – all parts of the Default network (32).

THE PATHOLOGY OF THE DEFAULT NETWORK

The carriers of the short alelle of the gene which encodes the protein transporter of serotonin (SERT s/s and s/l) have a higher activity of amygdala and hippocampus in resting state, possibly reflecting a process of permanent simulation and monitoring of activity. Hippocampus is part of the Default network, while amygdala is co-opted by this network during some processings. In addition, these people display rumination – a characteristic of a malfunctioning of “introspective” (Default) network (33). Default network is over-activated on patients with major depressive disorder when they have only to passively watch stimuli with negative valence, suggesting possible abnormalities in the automatic processing of negative stimuli (31). One of the most relevant recent descoveries is the competition between attention focused on task and processes which support stimuli independent thoughts (SIT). During cognitive tasks, occasional thoughts unrelated with the task can emerge. As many of these SIT emerge during a task, as much the performance in that task decreases. The emergence of SIT is associated with activity in Default network and rising the difficulty of the task, hence of attentional demands, leads to fewer SIT (6). Suppression of SIT (or rumination) by focusing on a difficult task is used in the therapy of some mental disorders like depression and anxiety, depressive patients being characterized by the tendency to manifest SIT which interferes with their performance in executive tasks (6, 34). On depressed patients, was described an over-activation of: supplementary motor and premotor areas (BA 8, 6), dorsal anterior cingulate cortex (BA 32), medial prefrontal cortex (BA 10), and lateral parietal cortex during tasks which imply the voluntary control over negative stimuli (when subjects were asked to give a positive valence to some aversive images) and additionaly a lack of deactivation of Default network, including hippocampus, parahippocampal gyrus and amygdala. So, the failure of depressed people to suppress activity of Default network through activation of an atentional network (see the next chapter) interferes with their ability to control negative thoughts and emotions (31). The Default network presents abnormalities also on patients with schizophrenia, Alzheimer disease and autism (14).

DEFAULT NETWORK VS THE NETWORKS OF ATTENTION

During performance in cognitive tasks requiring attention two types of brain responses may occur: a specific set of frontal and parietal regions manifest an increase of activity (called "positive zones"), while a different set of regions including posterior cingulate cortex, inferior lateral parietal and medial prefrontal cortex (called „negative zones"), are decreasing their activity. This dichotomy is getting more accentuated with rising the attentional demands of the task – the activity in the "positive zones" gets an extra boost, while the activity in the „negative zones" even more decreases (2, 3, 4, 5, 6). The momentary lapses in attention affects the goal-oriented behavior, sometimes with dramatic consequences. These lapses begin with the reduction of pre-stimulus activity in anterior cingulate cortex and right prefrontal regions involved in the attentional control. The deficit in stimulus processing during attentional lapses is characterized by remaining in the activation state of the Default network, while overcoming the lapses is characterized by the rising of activity in right inferior prefrontal gyrus (BA 44, 45) and right temporo-parietal junction (BA 7, 40, 39)(35). External sensorial stimuli are more likely to be perceived if activity in the ventral and dorsal attentional networks is higher with 3 seconds before their presentation and, by the contrary, are unlikely to be perceived if the activity in Default network is higher with 3 seconds before their presentation (36).

Studies using Independent Component Analysis technique (ICA) which evidentiates the intrinsec connectivity between neuronal networks (ICN) have revealed the existence of two anti-correlated networks, both of them separated by the Default network (37). First – named "ventral attentional network" (or "salience processing network", or "cingulo-opercular network") comprises the lateral orbitofrontal area (BA 47/12) and anterior insular cortex, dorsal cingulate cortex/paracingulate cortex, pre-supplementary motor area (BA 8), amygdala, ventral striatum, hipothalamus, dorsomedial thalamus, PAG, and substantia nigra/VTA. This network processes interoceptive/vegetative information, the emotional dimension of pain, empathy towards others' pain, hungry, pleasant touch, music, faces of beloved ones, and social rejection. People with a stronger connectivity between dorsal anterior cingulate and the rest of the network manifest an intense anticipatory anxiety (37). The second network – named "dorsal attentional network" (or "fronto-parietal network", or "executive control network") comprises the dorsolateral prefrontal cortex (BA 46), ventrolateral prefrontal (BA 45), caudal cingulate cortex/pre-supplementary motor area (BA 32, 8), lateral parietal cortex and intraparietal (BA 7), dorsal anterior caudate nucleu and anterior thalamus. This network deals with sustained attention and voluntary switching of attention, working memory, action selection but also the suppression of action. People with a stronger connectivity between intraparietal sulcus and the rest of the network have a superior performance in executive tasks (37). Using resting state functional connectivity MRI (rs-fcMRI) which evidentiates the regions of grey matter functionally connected in resting state, Dosenbach et al. (38) found two networks dictinctly involved in initiation, maintenance and control of behavior. Hence, the cingulo-opercular network including dorsomedial prefrontal/dorsal cingulate area, lateral orbitofrontal / anterior insula and fronto-polar cortex (BA 10), is involved both in initiation/preparing of behavior, and in maintenance of execution rules, and monitoring/processing of feedback. The fronto-polar area is responsible for implementing of complex set of rules and strategies. The second network, fronto-parietal, comprises intraparietal sulcusul (IPS), precuneus, dorsal cingulate cortex and dorsolateral prefrontal and is involved in initiation of control over behavior, assuring flexibility and voluntary switching of attention.

Various studies confirmed the existence of these networks. Hence, the dorsal attentional network was found to comprise the following regions: intraparietal sulcus (BA 7), superior parietal lobule (BA 7), pre-supplementary motor area and the region anterior to it (BA 8, 9), frontal eye field (BA 8) and right middle frontal gyrus (BA 9, 10, 46). It is involved in visual search tasks, visual trakking, working memory, waiting for the occurence of a stimulus, monitoring the environment/behavior, cheking the similarity between the action and its goal/target, and also in intentionally recolection of memories related with the goal of the action (39). These two attentional networks are superimposed at the level of middle frontal gyrus and inferior frontal gyrus (BA 46, 45)(6). These networks exist even in the resting state, functioning in an anti-correlated manner, so they don't occure spontaneously instead representing dictinct neuronal trajectories with specific role, and operating by information exchange and transfer (6). Both networks are activated in the so called "extrospective state" (by oposition with the "introspective state"). The regions activated in the extrospective state are those normaly involved in top-down and bottom-up attentional processes, working memory, response selection depending on the goal or the rule, and mentally representing the sequences of an action (5, 6). The R2 network of Mantini et al. (7) largely corespondes to the extrospective/dorsal and ventral attention networks and comprises intraparietal sulcus (IPS)(BA 7), frontal eye field (BA 8), bilateral middle frontal gyrus (BA 10, 9, 46) and right inferior frontal (BA 45, 44). The cerebral rythms evoked by this network are alfa and beta. This network is separated by the visual cortex (part of R3 network) which whom is coupled with during tasks requiring attentional processing of visual stimuli. The top-down processing of target which sould be searched by criteria held in working memory is executed first by lateral prefrontal (BA 10, 9, 46) and frontal eye field (BA 8) and after by intraparietal area (BA 7), all of them part of the dorsal attention network (40). This dorsal network deals also with figure-backgound delimitation (41). Electrophysiology studies coupled with imaging techniques have shown that the syncrony between frontal and parietal regions present middle frequency waves (22-44 Hz) during top-down tasks, reflecting the transmission of signals in the entire brain and communication-collaboration between various distant regions, while during bottom-up tasks occure especially high frequency waves (35-55 Hz) reflecting local interactions between neighbour regions (40). High fidelity rs-fc RMRI techniques indicated that the structures part of the dorsal network are also part of what is sometimes called "cognitive/associative network" including: precuneus (BA 31/7), inferior parietal lobule (especially angular gyrus), dorsolateral prefrontal/middle frontal gyrus (BA 9/10/46), frontal eye field (BA 8) and medial prefrontal cortex (BA 8 and adjacent BA 32). This network is involved in monitoring the information from the working memory and real time action planning (42).

THE EFFECT OF TRAINING UPON THE ATTENTIONAL NETWORKS

Studies using Granger Causality Analysis technique (GCA) have revealed that the dorsal attention network, the ventral attention network and the Default network are connected through the ventral one, especially through the right anterior insular cortex. GCA indicated that right anterior insula – part of the ventral network – represents a functional node which connects the dorsal executive network with Default network. It receives in-puts from parietal region and activates the anterior cingulate which whom it has strong connections, and which on his turn, activates the dorsal network, the last one implementing the executive control. These circuit operates regardless of the type of task or sensorial modality (43). The right insular cortex-cingulate cortex region (or cingulo-opercular) has a fundamental role in conflict detection, errors detection, and, more general, in adjusting the behavior to changes occured in environment or in task demands, the cingulo-opercular network implementing the shifting from one state to the other (43). It intervenes whenever an action should be initiated or when an existing pattern of actions should be modified or halted. It decides if an action should be initiated in the following situations: a) rutine processing of the stimuli fails to generate suficient data in order to trigger a response – for instance selecting between two paths of actions in response to an ambiguous stimulus; b) suddenly appears a new reason for action; and c) generating some environment exploring actions. In any of these situations this network suppress the rutine stimulus-response control, commuting to volitional control (22). On children below 9 years old the attention networks are connected on the dorsolateral prefrontal and fronto-polar level, the dorsomedial prefrontal/dorsal anterior cingulate region being strongly connected with the fronto-parietal network. Moving toward adolescence, a segregation between medial prefrontal/dorsal cingulate and fronto-parietal network appear, along with the integration of the first into the cingulo-opercular network. On adults, difficult cognitive tasks (like Stroop or dual processing tasks) can lead to a re-sincronization similar to that observed in children between fronto-parietal network and cingulo-opercular network, re-sincronization which disapppears with practice (44). Rueda et al. (45) realised an experiment on 4 respectively 6-year-old children exposed to a cognitive training procedure consisting in working memory tasks, conflict resolution tasks and inhibitory control tasks – 5 sesions during 3 weeks. The training has the effect of rising the amplitude of N200 potential in frontal areas (probably rostral cingulate cortex) in response to incongruent sequences of conflict resolution task in 4 years children, while in 6 years children the effect was observed especially in dorsal anterior cingulate cortex (part of ventral attention network), suggesting that development and/or training has an anterior to dorsal trajectory into the anterior cingulate. The training proved to be more relevant for those children with lower abilities in voluntary control and more extroverts (impulsive), similar results being observed also on children with ADHD (45). The experiments conducted on adults revealed also that cognitive training leads to alterations of the cerebral activity, probably on plastic nature. Olesen, Westerberg and Klinger (46) conducted a cognitive training lasting 20, 24 and 30 days using some working memory tasks. After training the following modifications were recorded: a rising in activity in left middle frontal gyrus (BA 10, 9, 46), bilateral superior parietal cortex (BA 7), intraparietal cortex and right inferior parietal, the head of caudate nucleus and thalamic pulvinar nucleus – all parts of the dorsal fronto-parietal network. Along with this increase of activity it was also noticed a decrease of activity in right cingulate sulcus (BA 32, 24), right inferior frontal sulcus (BA 45, 44)(both part of the ventral attention network) and left postcentral gyrus (BA 5)(46). These results indicate the relevance of cognitive training for treatment of developmental disorders and also for optimizing the mental performance on healthy adults.

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