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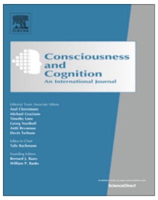

Review article

A role for the anterior insular cortex in the global neuronal workspace model of consciousness

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According to the global neuronal workspace model of consciousness, consciousness results from the global broadcast of information throughout the brain. The global neuronal workspace is mainly constituted by a fronto-parietal network. The anterior insular cortex is part of this global neuronal workspace, but the function of this region has not yet been defined within the global neuronal workspace model of consciousness. In this review, I hypothesize that the anterior insular cortex implements a cross-modal priority map, the function of which is to determine priorities for the processing of information and subsequent entrance in the global neuronal workspace.

Contents

1. Introduction

As the research on the neuronal correlates of consciousness (NCC) progresses (Bisenius, Trapp, Neumann, & Schroeter, 2015; Koch, Massimini, Boly, & Tononi, 2016), it is more and more important to develop a general model integrating these different correlates into a unified view of the functioning of consciousness (Block et al., 2014; Boly et al., 2013; de Gardelle &

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Kouider, 2009). One of the main integrative models, initially suggested by Baars (1988) and developed in cognitive neuroscience, mainly by Stanislas Dehaene and colleagues (Dehaene, 2014; Dehaene & Changeux, 2011; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Dehaene & Naccache, 2001), is called the "Global Neuronal Workspace" (GNW) model of consciousness. According to the GNW model, consciousness is the result of the global broadcast of information throughout the cortex. A "global neuronal workspace", constituted by interconnected high-level cortical regions such as the dorsolateral prefrontal cortex and the inferior parietal cortex, enables the global broadcast of information (Dehaene & Changeux, 2011).

The anterior insular cortex (aI) is an informational hub (Sterzer & Kleinschmidt, 2010; Touroutoglou, Hollenbeck, Dickerson, & Barrett, 2012; Uddin & Menon, 2009) and appears as a consistent neural correlate of consciousness across different experimental paradigms (Bisenius et al., 2015). But the different functional roles of the aI have not yet been integrated in the global neuronal workspace model of consciousness. Here, I suggest a functional role for the aI in a global workspace architecture. The aI has recently been hypothesized as a central component of the "salience network" (Goulden et al., 2014; Menon, 2015; Menon & Uddin, 2010). On this model, the role of the aI is to detect salient stimuli in order to determine whether stimuli should receive further cognitive processing and to facilitate access to working memory resources (Menon, 2015). My hypothesis is that the aI detects the relevance of stimuli across modalities and determines which stimuli need to be prioritized for entry in the GNW and sustained by top-down attention depending on the current goals at hand. The aI plays the role of a cross-modal priority map determining priorities of competing representations to reach conscious access.

2. The global neuronal workspace

In this paper, I will be primarily concerned with "access-consciousness", defined by Block (1995) as the availability of particular information for cognitive processes such as rational decision-making, control of action, reasoning, and verbal report. In the typical cases, consciously accessed information is also reportable. While some processes are conscious in this sense, most of our cerebral processes remain unconscious. What are the differences between conscious and non-conscious processing of information? The "Global Neuronal Workspace" model, first developed by Baars (1988), tries to answer this question. The central claim of the theory is that "conscious access is the selection, amplification, and global broadcasting, to many different areas, of a single piece of information selected for its salience or relevance to current goals" (Dehaene & Changeux, 2011).

This model predicts two phases through which a stimulus becomes consciously accessed (Dehaene & Changeux, 2011; Dehaene & Naccache, 2001). First, between 100 and 300 ms, the stimulus is non-conscious and climbs up a hierarchy of sensory processors: these processes contribute only to the non-conscious construction of the percept. This first phase is identical whether or not the stimulus is consciously accessed. In the second phase, if the stimulus is strong enough (e.g., in the case of a visual stimulus: duration, luminance and contrast) and/or corresponds to the task at hand, its representation will be sustained by top-down attention and selected for conscious-access (Dehaene et al., 2006). This top-down attention process entails a long-distance phase synchrony between the fronto-parietal network and the sustained sensory areas. Once this long-distance synchrony happens, the relevant stimulus is access-conscious, i.e., available for a broad palette of cognitive processes such as verbal report or decision making (Fig. 1).

The two main predictions resulting from this model have been verified through different experimental paradigms. First, we observe an all-or-none, late (from 300 ms) and sustained firing in the fronto-parietal network constituting the global workspace only when subjects are conscious of a stimulus across different modalities (Conscious/Unconscious visual stimuli (stimulus masking): Del Cul, Baillet, & Dehaene, 2007; Del Cul, Dehaene, Reyes, Bravo, & Slachevsky, 2009; Dehaene & Naccache, 2001; Fisch et al., 2009; Gaillard et al., 2009; Attentional blink: Sergent & Dehaene, 2004; Sergent, Baillet, & Dehaene, 2005; Williams, Visser, Cunnington, & Mattingley, 2008; Conscious/Unconscious tactile stimuli: Boly et al., 2007; Conscious/Unconscious sound: Sadaghiani, Hesselmann, & Kleinschmidt, 2009; Conscious/Unconscious error: Charles, Van Opstal, Marti, & Dehaene, 2013; van Gaal, Lamme, Fahrenfort, & Ridderinkhof, 2011; Binocular Rivalry: Sterzer, Kleinschmidt, & Rees, 2009). Second, conscious stimuli (and not unconscious ones) induce long-distance synchrony at beta and gamma frequencies and a late P3b wave in the same time-window (Bekinschtein et al., 2009; Del Cul et al., 2007; Doesburg, Green, McDonald, & Ward, 2009; El Karoui et al., 2015; Fisch et al., 2009; Gaillard et al., 2009; Hipp, Engel, & Siegel, 2011; Lange, Halacz, van Dijk, Kahlbrock, & Schnitzler, 2012; Melloni et al., 2007; Schurger, Cowey, & Tallon-Baudry, 2006; Sergent et al., 2005; van Aalderen-Smeets, Oostenveld, & Schwarzbach, 2009; Wyart & Tallon-Baudry, 2009). Interestingly, along the lines of these results, patients with perturbed long-distance connectivity due to multiple sclerosis show abnormal conscious perception of masked stimuli while subliminal priming is identical to control subjects (Reuter et al., 2007, 2009). Consistent with this data, studies using TMS over parietal or prefrontal cortices show that it can cause the disappearance of a stimulus from consciousness (Kanai, Muggleton, & Walsh, 2008; Rounis, Maniscalco, Rothwell, Passingham, & Lau, 2010). Del Cul et al. (2009) also observed an elevated threshold for conscious access in patients with prefrontal lesions. Evidence in favor of the GNW also comes from studies of patients in vegetative states (patients with preserved arousal but without behavioral signs of awareness) and minimally conscious states (patients with purposeful behavior but unable to communicate). A difference between vegetative state patients and minimally conscious state patients seems to be the absence of backward connectivity stemming from the frontal cortex (Boly et al., 2011), but see King, Bekinschtein & Dehaene (2011). Although brain activity in vegetative state patients is similar to sleep and anesthesia, patients in vegetative state have

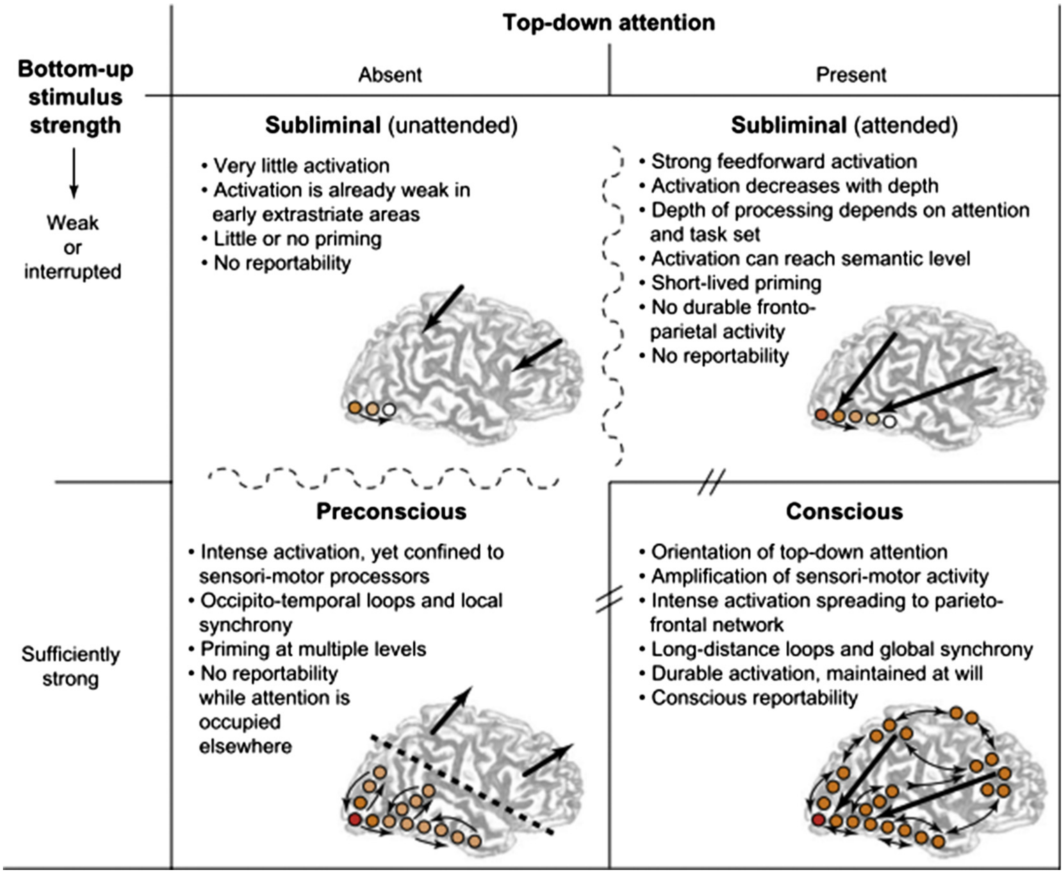

Fig. 1. Source: Dehaene et al. (2006) - According to the GNW model, a stimulus is selected to enter in the global workspace (and hence to become conscious) depending on two factors: the bottom-up strength of the stimulus and selection by top-down attention.

impaired fronto-parietal functions (Laureys, 2005; Laureys et al., 2000, 2002). Crucially, while long-distance functional connectivity is impaired in vegetative state patients, it is preserved in minimally conscious state patients: this difference in long-distance connectivity could account for the difference between the two conditions (Boly, Damas, & Lamy, 2004; Boly et al., 2008). Moreover, presence or absence of the P3b can be used to efficiently assess the presence of consciousness in noncommunicating patients (Faugeras et al., 2011, 2012; Schnakers et al., 2009; Sergent et al., 2017;Vanhaudenhuyse, Laureys, & Perrin, 2008).

Certainly the most contentious claim of the GNW theory is that attention is necessary for conscious access. The theory does not claim that top-down attention is *sufficient* for consciousness: attention can amplify the processing of stimuli that remain unconscious (Kentridge, Nijboer, & Heywood, 2008). Moreover, proponents of the GNW theory also recognize that, in simple displays, attention is not necessary for conscious access (Dehaene & Changeux, 2011; Wyart & Tallon-Baudry, 2008). Hence, top-down attention and conscious access are different processes. Proponents of the GNW theory claim, nonetheless, that in most conditions, when multiple stimuli compete for access to consciousness, selection by attention is necessary (Dehaene & Naccache, 2001; Dehaene & Changeux, 2011), as shown by inattentional blindness (Mack & Rock, 1998), the attentional blink (Dux & Marois, 2009; Martens & Wyble, 2010; Sergent & Dehaene, 2004; Sergent et al., 2005), and change blindness (Jensen, Yao, Street, & Simons, 2011; Niedeggen, Wichmann, & Stoerig, 2001; Simons & Ambinder, 2005). Despite this evidence, numerous authors claim that there can be awareness in cluttered displays in the absence of attention (Block, 2011; Bronfman, Brezis, Jacobson, & Usher, 2014; Lamme, 2003; Van Boxtel, Tsuchiya, & Koch, 2010), mainly based on evidence from gist perception outside of the scope of attention (Li, VanRullen, Koch, & Perona, 2002; Reddy, Wilken, & Koch, 2004; Reddy, Reddy, & Koch, 2006). Nonetheless, it seems that perception of the gist of a scene *is* subject to inattentional blindness when attentional resources are properly engaged (Cohen, Alvarez, & Nakayama, 2011; Mack & Clarke, 2012; Mack, Erol, Clarke, & Bert, 2016; Persuh, Genzer, & Melara, 2012). Although the debate is far from resolved (see Aru & Bachmann, 2013; Bachmann, 2011; Cohen, Cavanagh, Chun, & Nakayama, 2012; Cohen, Dennett, & Kanwisher, 2016; Van Boxtel et al., 2010), one reasonable hypothesis could be that bottom-up attention without top-down attention, or a weak level of top-down attention, can sometimes be sufficient for transient *entrance* in the GNW, but that top-down attention is necessary to *maintain* relevant information in the GNW, thus providing full conscious-access to the relevant information.

This distinction between entrance and maintenance in the GNW could also help the GNW theory accommodate data showing that the P3b wave is not always a reliable neural correlate of consciousness. According to several research groups (Pitts, Metzler, & Hillyard, 2014; Pitts, Padwal, Fennelly, Martinez, & Hillyard, 2014; Silverstein, Snodgrass, Shevrin, & Kushwaha, 2015, but See Rutiku, Martin, Bachmann, & Aru, 2015; Naccache, Marti, Sitt, Trübutschek, & Berkovitch, 2016), the P3b wave can occur unconsciously and consciousness can occur without the P3b, thus providing a dissociation between these phenomena. Instead, they argue that the N200 wave or "visual awareness negativity" (VAN) is a more reliable neural correlate of consciousness (Koivisto & Revonsuo, 2010). A plausible interpretation of this data could be that both ERP are neural correlates of consciousness (Rutiku, Aru, & Bachmann, 2016).[1] The VAN could reflect initial selection by bottom-up attention, prioritization of the stimulus for conscious access (Donohue et al., 2016) and, under conditions of low load of the GNW, transient entrance in the GNW; while the P3b could reflect selection of a stimulus for entrance in the GNW, and maintenance of relevant information by top-down attention.

Hence, across many studies in different paradigms, conscious processing involves a late, all-or-none amplification of the relevant sensory representations, an increase in long-distance phase synchronization between the fronto-parietal network and the relevant sensory areas (particularly in the beta and gamma range), top-down attention, a global P3b wave and the "ignition" of the fronto-parietal network, as predicted by the GNW theory (Dehaene, 2014). Although there are still debates about the activity of the frontal cortex as a necessary correlate of consciousness based on non-report experimental paradigms (Frassle, Sommer, Jansen, Naber, & Einhauser, 2014), about the P3b wave as a correlate of consciousness, and about the role of top-down attention for consciousness, I will consider that the GNW theory as presented above is a reliable framework to understand the functioning of consciousness. In the remaining of this paper, I develop a hypothesis on the role of the aI in the process by which a stimulus becomes conscious, or globally available, in a global workspace architecture.

3. The role of the aI in a global neuronal workspace architecture

The aI, located deep within the lateral sulcus of the brain, has traditionally been recognized as a multifaceted region, especially involved in interoception and somatosensory processing (Augustine, 1996). But recent studies describe new functional roles for the aI in a broad range of tasks. Craig (2009) reviews several studies showing a role for the aI across many different domains such as interoception, awareness of body movements, self-recognition, emotional awareness, uncertainty and anticipation, visual and auditory awareness of the moment, attention, perceptual decision-making and cognitive control (see also Kurth, Zilles, Fox, Laird, & Eickhoff, 2010; Nieuwenhuys, 2012; Sterzer & Kleinschmidt, 2010). In this review, I argue in favor of a common functional role in these different domains. My hypothesis is that one of the roles of the aI is to represent the relevance of sensory information across different modalities in order to determine priorities in the processing of information (by preparing the allocation of top-down attentional resources). Such a role is crucial in a global workspace architecture, as selecting *relevant* stimuli for further processing of information by a large number of systems is one of the main function of consciousness on this model. Hence, on my view, the aI implements a cross-modal *priority map* whose functional role is to determine priorities in the processing of information across modalities in order to decide whether information must be prioritized to enter the global workspace or not.

Stimuli are selected and represented in salience maps (Koch & Ullman, 1985; Itti & Koch, 2000; Walther & Koch, 2006), there is evidence that this selection operates early in the processing of information in areas V1 (Li, 2002). A salience map is a topographical map created for the allocation of top-down attention to representations of objects in the environment on the basis of their salience (Koch & Ullman, 1985). Salience is the physical distinctiveness of an object, defined by its physical properties, such as color, contrast or shape. Crucially, salience is determined independently of the internal mental states of the observer (such as goals or background knowledge). Priority maps are similar to salience maps but they encompass more than the mere salience of the stimulus in order to select it for further processing. Rather than operating a selection depending on the physical salience of a stimulus, priority maps select information based on its *relevance* in order to determine whether the processing of information should be prioritized or not (Fecteau & Munoz, 2006). As such, a priority map represents the general value of a stimulus for the organism depending on background knowledge and the task at hand. A priority map thus integrates sensory inputs, goals held in working memory, and background knowledge in order to establish the level of priority of a representation for further cognitive processing (Awh, Belopolsky, & Theeuwes, 2012; Fecteau & Munoz, 2006; Serences & Yantis, 2006; Yantis & Hillstrom, 1994) (Fig. 2). On this model, the processing of information represented as highly relevant is prioritized. As such, a priority map enables the determination of whether or not a representation should be prioritized to enter the GNW depending on its relevance for the organism considering its current goals and background knowledge.

Crucially, a priority map must be multimodal. As noted by Ptak (2012):

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[1] As noted by Rutiku et al. (2016), it is probably too early to know whether the P3b wave is a consequence of consciousness or a real NCC. Hence, if fronto-parietal activations, the P300 wave and gamma-band activity all seem to be NCC, it is still difficult to disentangle NCCs from consequences of consciousness, prerequisites of consciousness or task-related functions such as introspection (Aru, Bachmann, Singer, & Melloni, 2012; De Graaf, Hsieh, & Sack, 2012; Sergent & Naccache, 2012). Hopefully, future research will be careful about what is considered as an NCC by developing new experimental paradigms (such as non-report paradigms) (Overgaard & Fazekas, 2016; Tsuchiya, Wilke, Frässle, & Lamme, 2015).

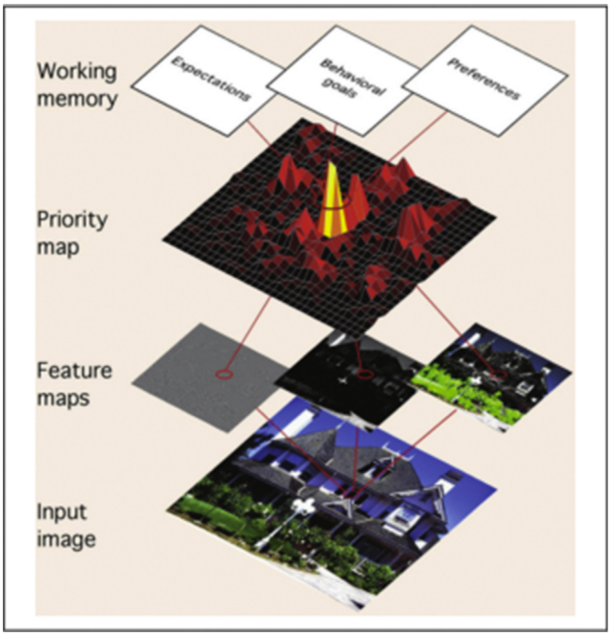

Fig. 2. Source: Ptak (2012) - On this model of computation of processing priority, a priority map is created by combining feature maps and top-down signals or high-level representations such as goals or expectations. Attention is oriented to the most relevant features represented on the priority map in order to prioritize the processing of relevant information by allowing it to access the GNW.

> "Because priority is an abstract quality of environmental stimuli that reflects the integration of a multitude of sensory signals, brain regions computing priority should be capable of multi sensory integration" (p. 503).

In order to allow for the flexible allocation of the processing resources offered by the GNW between incoming information from different modalities, a priority map must be multi-modal.

3.1. The aI: a cross-modal informational hub

If the aI is a cross-modal priority map, the aI should act as a central informational hub in the brain, receiving inputs from different sensory modalities such as the auditory and the visual system, but also information from the internal environment (interoception or emotions), in order to accomplish its role in representing relevance and determining processing priorities across modalities. The growing neurophysiological literature on the role of the aI strongly suggests that this is the case and that the aI is one of the main informational hubs of the brain. Indeed, several studies show that the aI integrates information from all sense modalities (Bamiou, Musiek, & Luxon, 2003; Butti & Hof, 2010; Downar, Crawley, Mikulis, & Davis, 2000; Nieuwenhuys, 2012; Sterzer & Kleinschmidt, 2010). It has also been hypothesized to operate cross-modal interactions by mediating the exchange of information across different sensory areas (Calvert, 2001). These results are also supported by studies using optogenetic techniques on a mouse model, suggesting that the aI is necessary for the cross-modal integration of sensory information (Gogolla, Takesian, Feng, Fagiolini, & Hensch, 2014).

Furthermore, the aI is part of the "rich club" network (Senden, Deco, de Reus, Goebel, & van den Heuvel, 2014; van den Heuvel & Sporns, 2011), such regions of the brain are characterized by dense anatomical connectivity with other parts of the brain and are amongst the most metabolically active regions (Grayson et al., 2014). In such a rich interconnected architecture, the aI would be one of the central informational hubs of the GNW. These informational hubs are crucial in a global workspace model, as they allow for the dynamic coupling of neural signals and for dynamic cooperation and competition among otherwise segregated information (Cocchi, Zalesky, Fornito, & Mattingley, 2013; de Reus & van den Heuvel, 2013). These studies suggest that the aI could play the role of an informational hub across different sense modalities. As such, it has been hypothesized by Umarova et al. (2010) that the aI could be involved in the cross-modal integration of information needed for conscious perception. As a part of the "salience network" (Menon, 2015), network analysis shows that the aI is one of the brain region that has the most important tendency to interact with brain regions outside its community (high temporal flexibility) and maintains a high level of centrality over time, thus revealing that the aI could be an informational hub, the function of which is to facilitate interaction between different networks of the brain (Chen, Cai, Ryali, Supekar, & Menon, 2016).

Moreover, along with sensory information, the aI is critical for awareness of interoception, the sense of the physiological condition of the body (Craig, 2003, 2011) and for awareness of emotions (Gu, Liu, Van Dam, Hof, & Fan, 2013; Gu, Hof, Friston, & Fan, 2013; Lindquist, 2010). The fact that the aI is particularly activated when pain is involved is also in favor of this hypothesis, as pain is a particularly relevant event that should be prioritized. This role for the aI would explain why it was considered for a long time as a part of the brain exclusively dedicated to interoception (Augustine, 1996). Interestingly, and in accordance with my hypothesis, the aI does not seem to be central for interoception in and by itself, the *posterior* insula is the central interoceptive cortex (Frot & Mauguière, 1999; Frot, Magnin, Mauguière, & Garcia-Larrea, 2007). Rather, the aI:

> "*re*-represents and integrates these interoceptive representations with exteroceptive sensory information. The integration of inter- and exteroceptive information in the aI ostensibly serves to generate the subjective experience of emotion" (Nguyen, Breakspear, Hu, & Guo, 2016).

Research by Frot, Faillenot, and Mauguière (2014) is consistent with this hypothesis: pain is first processed in the posterior section of the insula, and then conveyed to the aI. Hence, as a central informational hub, the aI would re-represent information on a cross-modal priority map, thus operating the integration between the external and the internal milieu (Nguyen et al., 2016). Along with its role in proprioception, the insular cortex also has a critical role in emotional awareness (Craig, 2009, 2010, 2011; Gu, Hof, et al., 2013; Jones, Ward, & Critchley, 2010; Seth, Suzuki, & Critchley, 2012; Singer, Critchley, & Preuschoff, 2009). On the main model of the relations between the aI and emotional awareness, the aI functions as an interface integrating high-level representations and interoceptive inputs, thus generating a signal representing the subject's emotional state (Gu, Hof, et al., 2013; Seth et al., 2012).

Supporting these findings is the additional fact that the aI has been identified as a "master switch for consciousness" (Blumenfeld, 2014). Although this review paper focuses on consciousness in its transitive sense (being conscious *of* something), it should be noted that the aI could also have a role in states of consciousness, or consciousness in its intransitive sense (being conscious, rather than being in a coma for example). Koubeissi, Bartolomei, Beltagy, and Picard (2014) discovered that an electrical stimulation between the aI and the claustrum, a small area next to the insular cortex,[2] can lead to the (reversible) disappearance of consciousness with amnesia. One hypothesis could be that the electrical stimulation of the claustrum and aI leads to an overload of the GNW, thus causing increased synchrony between several modules of the GNW (Bartolomei & Naccache, 2011; Bartolomei, McGonigal, & Naccache, 2014). A sudden increase in synchrony would then lead to the disappearance of consciousness. Indeed, increased synchrony between long-distant areas of the brain is known to be involved in epileptic seizures (Jiruska et al., 2013). This interpretation of the data would also be consistent with Picard et al.'s proposal that the aI could be responsible for ecstatic epileptic seizures (Gschwind & Picard, 2016; Picard & Craig, 2009; Picard & and Kurth, 2014).

I conclude, from the fact that the aI integrates different sensory information across modalities (along with emotions and interoception), is part of the rich club network, and is a "master switch for consciousness", that the aI is a good candidate to implement the cross-modal priority map needed for the flexible modulation of information that needs to enter in the GNW.

3.2. The aI: at the heart of the ventral attention system

The role of the aI (specifically the right aI) is also well known for bottom-up attention. Indeed, the aI is "at the heart of the ventral attention system" (which is considered to implement bottom-up attention) and is involved in attentional capture (Eckert et al., 2009). Accordingly, Nelson et al. (2010) discovered that the aI is involved in task-control signals (i.e. task initiation and task maintenance signals) and determines the focus of attention depending on these tasks. Thus, Nelson et al. (2010) hypothesize that the aI could integrate task-related top-down information and sensory feedback in order to determine "adjustments in the top-down signals" (see also Dosenbach et al., 2006; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008). Hence, the aI is responsible for the interaction between bottom-up attention and top-down attention by its access to task-related information (Eckert et al., 2009; Touroutoglou et al., 2012), a role similar to that of a priority map.

Consistently with the hypothesis according to which the role of the aI is to implement a cross-modal priority map, the aI is also involved in the modulation of attention to multisensory stimuli (Bushara, Grafman, & Hallett, 2001; Bushara et al., 2003; Sterzer & Kleinschmidt, 2010). A recent study by Chen et al. (2015) further supports this hypothesis by providing direct evidence for the role of the aI in determining the allocation of attentional resources across different modalities (auditory/visual). Furthermore, as would be predicted if the aI integrates representations of relevance across modalities, the aI is consistently activated by the mismatch between different sensory modalities, such as visuo-tactile mismatch (Banati, Goerres, Tjoa, Aggleton, & Grasby, 2000) or asynchrony of speech and vision (Benoit, Raij, Lin, Jääskeläinen, & Stufflebeam, 2010; Miller, 2005). As this region plays a role in determining the distribution of attentional resources across modalities, its role as a cross-modal priority map thus acquires additional support.

3.3. The aI and the "salience network"

The aI was recently supposed to take a functional role, along with the anterior cingulate cortex, as a part of a "Salience Network" (Chen et al., 2016; Goulden et al., 2014; Menon, 2015; Menon & Uddin, 2010; Uddin, 2014). The aI functions as a

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[2] The claustrum is also an interesting region for consciousness, as it is one of the main informational hubs in the brain due to its connectivity (Torgerson, Irimia, Goh, & Van Horn, 2015), and has been named by Crick and Koch (2005) "the seat of consciousness". Research by Mathur (2014) or Goll, Atlan, and Citri (2015) recently hypothesized a role similar to the cross-modal priority map for the claustrum. Hence, additional research may lead to the idea that the aI and the claustrum interact in order to implement the cross-modal priority map.

bottom-up detector for salient events across different sensory modalities. According to this model, the aI is also responsible for the switch between different large-scale networks in order to "facilitate access to attention and working memory resources when a salient event is detected" (Menon & Uddin, 2010). The role of the aI is then to identify salient stimuli in the stream of continuous sensory information and send signals to the systems responsible for the allocation of top-down attentional resources to the relevant sensory representations (Menon, 2015). Hence, once the aI identifies a relevant stimulus, its representation is sustained by attentional resources, and it facilitates the disengagement of systems that are not directly relevant to the task at hand (Menon & Uddin, 2010).

On the salience network model, both the aI and the ACC are central nodes of the salience network. The aI has particularly strong connectivity and functional covariance with the ACC (Cauda et al., 2011; Chang, Yarkoni, Khaw, & Sanfey, 2013; Deen, Pitskel, & Pelphrey, 2011). The aI and ACC also share a particular type of neurons, which is almost unique to these regions: the von Economo neurons (Allman et al., 2011). The wide axons of the van Economo neurons are thought to allow the fast relay of information throughout the cortex: this particular cytoarchitecture is consistent with the cross-modal priority map hypothesis as it would allow the salience network to reorganize processing resources efficiently (Allman, Watson, Tetreault, & Hakeem, 2005; Raghanti et al., 2015). However, it should be emphasized that the aI and the ACC, despite their similarities, have distinct functional roles within the salience network. Although the ACC is thought to be involved in attention, especially attention for action (Posner, Petersen, Fox, & Raichle, 1988; Taylor, Rushworth, & Nobre, 2008), the aI is best suited to implement a cross-modal priority map. Indeed, while the aI is a multimodal hub receiving multisensory inputs, as reviewed above, the ACC does not seem to receive as many sensory information (Averbeck & Seo, 2008; Menon, 2015). The two regions also have distinct outputs: the ACC is closely related to response selection and conflict monitoring (Ide, Shenoy, Yu, & Li, 2013; Rushworth, 2008) and has rich projections to premotor and motor cortices (Morecraft & Tanji, 2009). On the contrary, the aI has little motor outputs. As suggested by Paus (Paus, 2001), the main role of the ACC is to enable appropriate behavioral responses to internal or environmental relevant events, but it may not be necessary to detect relevance across modalities. As such, the aI seems to be best suited to implement the cross-modal priority map. The ACC has an executive role and is a key component of the global neuronal workspace (Dehaene & Naccache, 2001; Dehaene et al., 2003), it allows the effective allocation of attention and preparation of appropriate behavioral responses once the aI has determined which stimuli are relevant (see Fig. 3). The interaction between the aI and the ACC is thus of fundamental importance in a global workspace architecture.

According to the salience network model, the role of the aI is to determine which stimulus deserves top-down attention based on present goals and to what degree these resources should be allocated to the stimulus, considering its salience and relevance to the task (a role that is very similar to the role of a priority map). Furthermore, according to the salience network theory, the activation of the aI and the subsequent activation of the ACC to regulate attention by a control signal correlates with the N2b wave (between 200 and 300 ms after the stimulus), an event-related potential that is called the "awareness negativity" and is a reliable correlate of consciousness (Koivisto & Revonsuo, 2010). Consistent with the role of the aI as implementing a cross-modal priority map, disrupting the salience network also impairs task switching (Bonnelle et al., 2012; Jilka et al., 2014). I take the role of the aI in the salience network as evidence for the thesis according to which the aI implements a cross-modal priority map; indeed, the role of the aI in the salience network is similar to the hypothesized role that it would have in a global workspace architecture.

As would be predicted if the aI implements a cross-modal priority map, the aI is also involved in conscious perception of errors (Ham, Leff, de Boissezon, Joffe, & Sharp, 2013; Klein, Ullsperger, & Danielmeier, 2013; Ullsperger, Harsay, Wessel, & Ridderinkhof, 2010). Indeed, errors are particularly salient events the processing of which should be prioritized (Menon,

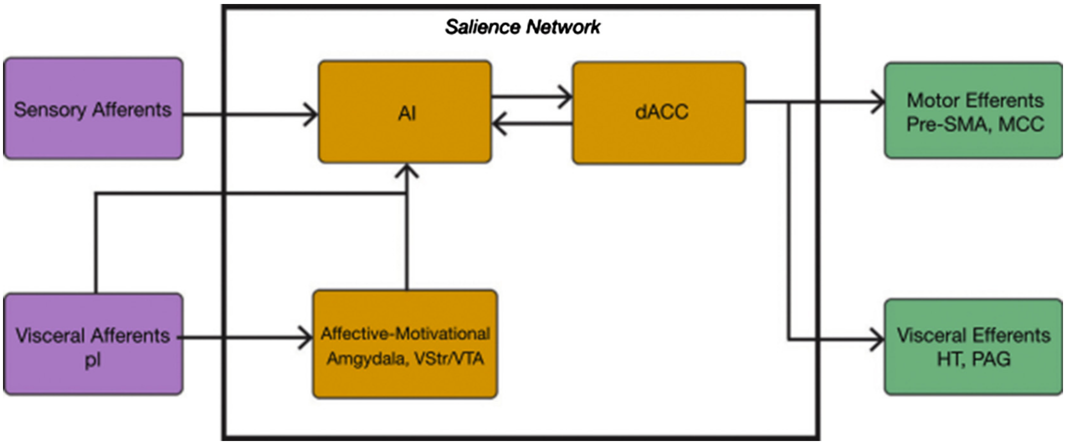

Fig. 3. Source: Menon (2015) - Main inputs and outputs of the salience network and functional differences between the aI and the ACC. The role of the aI is to implement a cross-modal priority map and to detect relevant stimuli. The role of the ACC is to prepare appropriate behavioral response and reorganize cognitive processing resources.

2015). For example, in an anti-saccade task, the activity of the aI varies with consciously perceived and non-consciously perceived errors (Klein et al., 2007). Along the lines of these results, recent evidence demonstrates that the aI is particularly activated by surprising tactile stimuli (i.e., stimuli that should be prioritized) and could engage and coordinate activity between sensory and attention-related brain areas in order to support the processing of these stimuli (Allen et al., 2016). Hence, the aI would provide a link between sensory areas and anterior areas of the GNW such as the ACC, coordinating the mechanisms responsible for the allocation of attentional resources and areas processing relevant sensory information from internal and external environment.

3.4. Integrating external and internal milieu: aI and self-consciousness

Although this paper focuses on access-consciousness, it should be mentioned that the aI has also been hypothesized to play a role in self-consciousness (Craig, 2009, 2014). Self-consciousness could be defined as the subjective feeling that all the experiences that I have are *my* experiences. In an excellent review of the literature on the role of the aI, Craig (2009) hypothesized that the aI could be the seat of self-consciousness because it integrates the internal and external milieu. On this view, self-consciousness could be accomplished in the aI by binding information related to the self (interoception, emotions) with information coming from the external environment, thus creating a unitary awareness of *the self* having the experience (a similar theory has been developed by Damasio (2010)). Bodily awareness and the feeling of "presence" could be attributed to the integration of information concerning bodily states and prior beliefs in the aI (Seth et al., 2012; Seth, 2013). Although this hypothesis is still speculative, some data seem to provide evidence in favor of a role for the aI in self-consciousness. First, the aI is composed of "von Economo neurons" allowing a long-distance and fast connectivity within the aI and between the aI and other regions of the brain (Nieuwenhuys, 2012). These neurons have been found only in species able to pass the standard mirror test for self-recognition (such as elephants and macaques for example) (Critchley & Seth, 2012; Evrard, Forro, & Logothetis, 2012; Hakeem et al., 2009). Second, schizophrenia, one of the psychotic disorder that typifies disturbance of consciousness and self-consciousness, is related to disturbance of connectivity with the aI and with impairments of van Economo neurons (Cascella, Gerner, Fieldstone, Sawa, & Schretlen, 2011; Manoliu et al., 2014; Moran et al., 2013; Palaniyappan, Simmonite, White, Liddle, & Liddle, 2013; Penner et al., 2016; White, Joseph, Francis, & Liddle, 2010). Third, disturbance of the aI could be involved in Cotard syndrome, in which patients claim that they do not exist or that parts of their body do not exist (Chatterjee & Mitra, 2015). These different empirical facts could provide evidence in favor of a role for the aI in self-consciousness; self-consciousness would then result from the integration of the internal and external milieu on a common cross-modal priority map, thus binding these different information together into an unified model of the conscious self. Disruptions of this mechanism would be involved in schizophrenia or Cotard syndrome.

Nonetheless, I want to distinguish my hypothesis according to which the aI plays the role of a cross-modal priority map from Craig's claim (Craig, 2009, 2014) that the aI could be necessary for self-consciousness or for conscious access. My claim is that the aI is necessary to efficiently allocate cognitive resources by determining processing priorities in order to regulate entry in the GNW. Hence, on my view, the aI is *not* necessary for conscious access. Indeed, recent case studies reported that bilateral insular lesions do not specifically impair conscious access or self-consciousness (Damasio, Damasio, & Tranel, 2013; Khalsa, Rudrauf, Feinstein, & Tranel, 2009; Philippi et al., 2012). In these studies, the two patients "M" and "Roger" are still able to perform correctly on self-recognition tasks despite bilateral insular lesions (Damasio et al., 2013; Philippi et al., 2012). Moreover, Feinstein et al. (2016) recently used a variety of measures of pain experience such as verbal report, facial expressions, vocalization or withdrawal reactions in a patient with impaired insula ("Roger"), in order to provide evidence that the aI is not necessary for conscious experience of pain. Across all measures, patient Roger showed preserved awareness of pain despite extensive bilateral damage to the insula.

Nevertheless, there are several questionable points in these studies. First, self-awareness is assessed by Philippi et al. (2012) and Damasio et al. (2013) on the basis of self-recognition tasks. But self-recognition could involve a broad prefronto-parietal network (Devue & Brédart, 2011; Keenan, Wheeler, Gallup, & Pascual-Leone, 2000), which is not entirely impaired in M and Roger. Moreover, as noticed by Gu, Hof, et al. (2013).

> patient Roger did exhibit deficits in certain aspects of interoceptive awareness, as reported in supplemental materials by Khalsa et al. (2009). For instance, he was unable to detect heart rate change at low doses of isoproterenol infusion, his response lag was significantly longer than controls, and his interoceptive awareness was greatly worsened after anesthetic application (Khalsa et al., 2009).

Hence, it could be that, although awareness is not abolished in these patients, conscious access to interoceptive and emotional information is still impaired. Once again, my claim is not that the aI is necessary for conscious access or self-consciousness (contrary to Craig, 2009). Rather, my claim is that the aI is necessary to regulate entrance in the GNW by assessing the relevance (or the processing priority) of competing representations from different sensory modalities.

In the case study by Feinstein et al. (2016), the patient Roger was still aware of his pain despite damage to the aI. Nonetheless, Roger reached his pain tolerance threshold faster than comparison subjects, his pain ratings were way higher than comparison subjects, he had intense pain vocalizations and was "unable to refrain from pain-related movements". This leads Feinstein et al. (2016) to hypothesize that "the missing regions in Roger's brain would impair his ability to control and downregulate his pain responses". Such data is consistent with the aI playing the role of a cross-modal priority map for conscious access. Indeed, Roger seemed unable to prevent his own pain to gain access to consciousness (for example by focusing

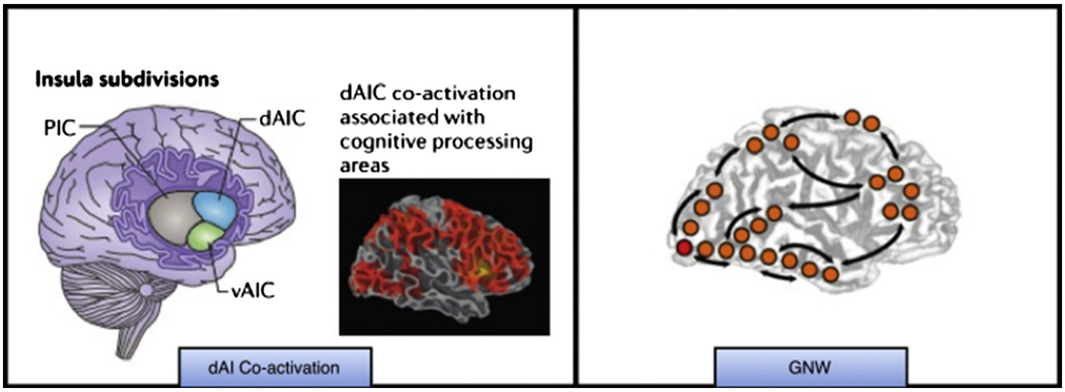

Fig. 4. Source: Uddin (2014) and Dehaene and Changeux (2011) - Brain areas correlated with the activation of the dorsal aI. These areas correspond almost exactly to the areas that are supposed to be part of the GNW.

his attention on something else, a strategy that could be available for other subjects). In other words, because of damages to the aI, Roger was unable to prevent a salient painful stimulus to gain access to consciousness by regulating the processing priority, or the relevance, of this stimulus. If this interpretation of the results is right, a prediction is that Roger should be unable to ignore particularly salient stimuli, even when these are unrelated to the task at hand. He should also be unable to detect non-salient stimuli, even when these are relevant for the task. Hence, a possible prediction is that, in patients with aI lesions, the threshold for conscious-access is disrupted such that salient but non-relevant stimuli necessarily enter in the GNW, and, on the contrary, non-salient but relevant stimuli are not prioritized for entrance in the GNW.

This interpretation of the data is consistent with studies on alexythimia, a condition characterized by impaired awareness of emotions (Aleman, 2005) which often co-occurs with schizophrenia (Fogley, Warman, & Lysaker, 2014). Alexithymia is associated with reduced aI activations and grey matter volume (Ihme et al., 2013; Silani et al., 2008), and a recent study by Hogeveen, Bird, Chau, Krueger, and Grafman (2016) shows that the extent of damage to the aI predicts alexithymia severity. If the aI acts as a cross-modal priority map, a possible interpretation of these results could be that patients with alexithymia are unable to detect subtle changes (such as interoceptive changes) in their experience because they do not categorize these changes as relevant, and are thus unable to adequately prioritize emotions for subsequent entrance in the GNW.

3.5. A role for the aI and the cross-modal priority map in a global workspace architecture

The link between the aI and the GNW is quite straightforward. First, the aI is a part of the fronto-parietal network constituting the GNW (Dehaene & Changeux, 2011) and is a common NCC (Bisenius et al., 2015). Furthermore, the aI has direct white matter connections to other key hubs of the GNW such as the ACC (Van Den Heuvel, Mandl, Kahn, & Hulshoff Pol, 2009) and the inferior parietal lobe (Uddin et al., 2010), allowing fast interactions and synchrony between the different hubs of the GNW. Also, the brain regions correlated with the activation of the dorsal aI, responsible for the integration of bottom-up and top-down information (a process that is crucial in the GNW model) are almost exactly the regions thought to be involved in the global workspace (Fig. 4). Furthermore, the timing in which the aI executes the switch between large-scale networks corresponds to the timing of the access of a stimulus to consciousness and generates the same event-related potentials. Indeed, the salience network (aI and ACC) is activated 200–300 ms after a salient stimulus and correlates with the appearance of the N2b/P3a wave, then, between 300 and 400 ms, top-down attention is allocated to the relevant sensory areas, the attentional shift is responsible for the apparition of the P3b wave (Menon & Uddin, 2010). This is the exact same time-window and event-related potentials as the ones found in the access of a stimulus to consciousness (Dehaene & Changeux, 2011; Dehaene, 2014). This data suggests that the process by which a stimulus is prioritized by the aI and receives top-down attention is the same as the process that results in the conscious access to a stimulus according to the GNW model of consciousness. These correlations between ERPs of conscious access and activity of the salience network are additional evidence in favor of the hypothesis that the aI implements a cross-modal priority map that determines which stimuli should be prioritized to enter in the GNW.

4. Conclusion

I conclude with some speculations on the general mechanism by which consciousness arises. My view is that the aI is a crucial functional component of the GNW: it implements a cross-modal priority map, the role of which is to determine processing priorities of stimuli across modalities for subsequent entrance in the GNW. On my view, once a stimulus is processed unconsciously during 200 ms, it is transferred to the aI, which determines its relevance compared to other competing stimuli in other modalities and determines the amount of top-down attentional resources that should be attributed to the stimulus. At this point, the relevant stimulus is prioritized and transiently enters the GNW, this process of selection correlates with the visual awareness negativity (N2). Then, from 300 ms, top-down attentional resources are allocated by recruiting the attentional networks and working-memory, resulting in the "global ignition" of the fronto-parietal network (and the P3b wave); this top-down attentional process then constitutes a re-afferent loop maintaining the relevant stimulus in the GNW. Hence, on this model, the aI would be the arbitrator of the competition to enter the GNW: its role would be both to determine which of the competing stimuli are relevant enough across all sensory modalities in order to be prioritized and integrate the GNW, and which stimuli should receive top-down attention in order to be maintained in the GNW.

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