

The hidden side of intentional action: the role of the anterior insular cortex

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Abstract Cognitive neuroscience research has begun to reveal the functional neuroanatomy of intentional action. This research has primarily pointed to the role of the medial frontal cortex for the voluntary control of behaviour. However, a closer inspection of the literature reveals that the anterior insular cortex (AIC) is also routinely activated in tasks that involve different aspects of intentional action. In the present article, we outline studies that have found AIC activation in various intentional action paradigms. Based on these findings, we discuss two hypotheses about the AIC's contribution to voluntary control. One hypothesis states that AIC is involved in forming intentions, by providing information about the internal states of the system. The alternative view suggests that AIC evaluates the outcomes of intentional action decisions that have been previously formed elsewhere. The limited evidence so far favours the evaluative hypothesis. AIC may provide interoceptive signals that play an essential role in evaluating the consequences of intentional action. AIC is therefore a key structure for the adaptive, affective training of the individual will, on which human society depends.

Keywords Intentional action · Anterior insular cortex · Interoception

Introduction

The question of how we can voluntarily control our behaviour is fundamental to our understanding of human nature. A common way to conceptualise voluntary or intentional action is to distinguish it from stimulus-guided behaviour where an action is triggered by the environment. We assume that there is a continuum that ranges from reflexive behaviour, exclusively determined by the stimulus, to behaviour that is completely undetermined by the stimulus, and therefore presumably is internally selected, and internally generated. Experimental psychology has long focussed primarily on stimulus-guided action. The ease of manipulating the stimulus means that an experimental approach can make good progress. At the same time, this knowledge seems to ignore aspects of voluntary control that seem to make us uniquely human. Recently, research on intentional action has made some methodological progress that allows voluntary control to be studied in a more scientific way than previously. In particular, brain imaging techniques have facilitated the investigation of mental processes that are not directly related to environmental events.

Voluntary control has been defined above in terms of internal selection and generation of action. However, several different kinds of information must be generated (Brass and Haggard 2008). For example, the pioneering experimental work of Libet et al. (1983) required participants to freely choose when to press a key. Most brain imaging studies on the *when* component of intentional action compare a situation where participants can choose

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the moment when to execute an action with a situation where the time point is externally given (Ball et al. 1999; Jenkins et al. 2000; Cunnington et al. 2002; Wiese et al. 2005). An interesting contrast between these two conditions is the timing of neural preparation: voluntary actions are routinely preceded by a characteristic rising negativity over frontal motor areas (the ‘readiness potential’), whereas externally-triggered responses are not (Jahanshahi et al. 1995). Another set of studies has focused on the intentional decision between different response alternatives or in other words the *what* component of intentional action (e.g. Lau et al. 2004a; van Eimeren et al. 2006; Mueller et al. 2007). In these experiments, participants usually have to choose between two or more response alternatives. The free choice between response options is compared to a situation where the response is determined by an external stimulus. In the case of simple choices between left and right hand actions, there is again a useful electrical signal of what decisions: the lateralised readiness potential. This is shown as an increased readiness potential in the hemisphere contralateral to the hand that makes the action, relative to the ipsilateral hemisphere. It appears after the onset of the readiness potential, but some 500 ms before action. Recently, we have argued that intentional action not only involves a decision *when* to act and *what* action to execute but also the decision *whether* to act or not. This *whether* component of intentional action has been investigated with paradigms where participants can freely decide to stop an ongoing behaviour in the last moment (Brass and Haggard 2007, 2008; Kuhn et al. 2009).

The literature on brain correlates of intentional action has emphasised the role of the fronto-median wall. In particular, a discussion has evolved whether intentional action is related to the rostral cingulate zone (RCZ) which extends dorsally from the anterior cingulate cortex (ACC), or is located in more posterior fronto-median wall areas, such as the preSMA (e.g. Lau et al. 2004a). This discussion is tightly linked to the question whether choice-related brain activation can be conceptually distinguished from conflict-related brain activity, since the RCZ is also consistently involved in conflict tasks (Lau et al. 2004a). Some recent data suggests an anatomical separation, with conflict represented more rostrally, and volition more caudally within preSMA (Nachev et al. 2005). Another brain region that has been related to intentional behaviour is the parietal cortex (Sirigu et al. 2004). Patients with parietal lesions have problems with the awareness of their intention to act, while parietal stimulation, like preSMA stimulation, can cause an ‘urge to move’ in the absence of actual movement (Fried et al. 1991; Desmurget et al. 2009).

However, when carefully looking at the brain regions that are activated in intentional action paradigms, it turns out that the anterior insular cortex (AIC) is also routinely

activated by intentional actions (Jahanshahi et al. 1995; Jenkins et al. 2000; Brass and Haggard 2007; Mueller et al. 2007; Kuhn and Brass 2009). From a neuroanatomical perspective, this is not very surprising given that the ACC is connected with the insula (Augustine 1996). Furthermore, coactivation in the ACC and AIC have been observed in a number of other domains such as conflict processing or pain processing (for an overview see Craig 2009; Medford and Critchley 2010). An involvement of AIC in intentional action also makes cognitive and neurophysiological sense. The defining feature of intentional action is that it is internally driven. The AIC seems to play a major role in interoceptive awareness (Craig 2002, 2009). Moreover, the concept of homeostatic design implies that humans and animals may act, in the absence of any external stimulus, to maintain an interoceptively-sensed internal equilibrium (Craig 2003). Thus, the internal generation of action in the frontomedian wall might well be linked to awareness of the internal milieu in the anterior insula. But how consistent is AIC activation in intentional action experiments? And what is its specific functional role? In this article, we will first discuss some studies that showed AIC activation in intentional action. This part will follow the distinction between the *what*, *when* and *whether* aspects of intentional action that we have outlined previously (Brass and Haggard 2008). Next, we will try to narrow down the functional role of the AIC for voluntary action. We will primarily contrast two opposing views: one account assumes that the AIC is involved in the choice process itself by providing interoceptive information to guide action selection. The alternative account proposes that the AIC is involved in processing the value of actions once they are made.

AIC activation related to the *when* and *what* aspects of intentional action

Studies investigating the *what* component of intentional action usually compare a situation where participants freely choose between response alternatives with a situation where a stimulus determines the correct choice. While these studies reliably identify activation in the fronto-median cortex, activation in the AIC was not always found (e.g. Lau et al. 2004a; van Eimeren et al. 2006). However, one study that yielded activation in the AIC was carried out by Mueller et al. (2007). Here, participants had to either freely chose between a left or a right response. In other conditions, they responded to the left or right stimulus. In contrast to most other studies on the *what* component of intentional action, this study controlled for stimulus and response properties. Strong bilateral activation was found in the middle part of the AIC (Talairach, left, x: -39, y: 5,

z : 6; right, 39, 8, 0). Studies on the *when* component of intention action also provide an inconsistent pattern of results regarding the involvement of the AIC. Most studies reported no activation difference in AIC for self-paced finger movements compared to acoustically or visually triggered movements (Ball et al. 1999; Cunnington et al. 2002; Wiese et al. 2005). However, a study by Jenkins et al. (2000) found bilateral AIC activation for the comparison of self-initiated key presses compared to externally-triggered key presses. This activation was located in the dorsal AIC with a z -coordinate of around 10 (Talairach, left, x : -36, y : 10, z : 12; right, x : 34, y : 18, z : 08). However, there was also anterior insular activation when the externally-triggered condition was compared to resting baseline, indicating that the AIC was not exclusively involved in the self-paced condition.

It is useful also to consider three other studies, which did not show AIC activations related to intentional action. In a study by Lau et al. (2004b), participants had to carry out a version of the Libet task. In one condition, they were instructed to attend to the intention to act and in the other condition they were instructed to attend to the movement. This study led to activation in the preSMA, the dorso-lateral prefrontal cortex and the intraparietal sulcus (IPS) but not to AIC activation. One could argue that if the AIC plays a crucial role in the decision to execute a specific behaviour by providing interoceptive awareness one would expect AIC activation in a condition where participants are explicitly instructed to attend to the decision. There are two additional fMRI studies that argue against a role of the AIC in the decision phase of intentional action. In a study by Soon et al. (2008), participants had to carry out a choice variant of the Libet task. They could freely choose when to press a left or a right key. Multivariate decoding was used to determine brain areas that allowed predicting the choice. While fronto-median brain areas predicted the decision seconds in advance, the AIC was not reported to carry any predictive information. The second study (Krieghoff et al. 2009) tried to dissociate the *when* and *what* decision of intentional action. Here, participants saw a cue that either determined the *when* and/or the *what* decision or left it open to the subject to choose. When analysing the decision phase both the *when* and the *what* decision led to fronto-median activation. However, no activation was found in the AIC.

To summarise, there is mixed evidence for the involvement of the AIC in the *what* and *when* decision of intentional action. Some studies identified AIC activation while other did not. Furthermore, studies that dissociated the decision phase from the execution phase did not find AIC, suggesting that the role of the AIC is not related to the intentional decision process. However, this conclusion has to be treated with care because it is only based on a failure

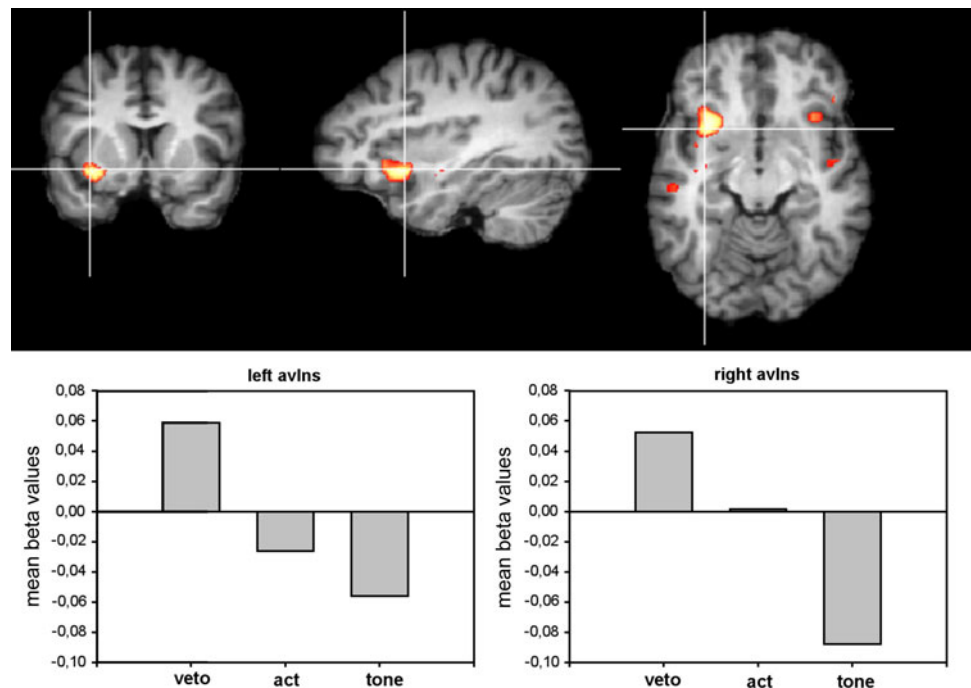
to find AIC activation in three studies. In general, it is crucial to be aware of methodological problems with identifying AIC activation from published work. Activation in AIC very often extends to the convexity of the inferior frontal gyrus (IFG). But if the z -maximum is located in the IFG, activation in AIC would be missed.

Intentional stopping and the AIC

There is extensive research on the role of the prefrontal cortex in inhibitory control. It has been argued that the right ventrolateral prefrontal cortex is crucially involved in response inhibition (Aron et al. 2004). Furthermore, lesion work and work on structural connectivity suggest that the anterior insula cortex is crucial as well (Hodgson et al. 2007; Forstmann et al. 2008).

Interestingly, explicit research on intentional stopping is relatively new. However, the first study that explicitly investigated intentional stopping yielded a very strong and relative selective activation in the AIC (Brass and Haggard 2007). Here, participants had to intentionally decide to execute an action but were instructed to stop this movement in the last moment in some trials. They were free to choose in which trials they vetoed the ongoing actions. Only three brain areas showed stronger activation when comparing the intentional inhibition of the action with the intentional execution (Fig. 1). The strongest activation was located in the left ventral AIC (Talairach, left, x : -31, y : 8, z : -6; right, x : 32, y : 17, z : -9). Furthermore, there was a weaker activation in the right AIC. Given the inconsistent results regarding AIC activation in studies investigating the *when* and *what* component of intentional action, this clear result merits further discussion. First, one has to keep in mind that participants were instructed to initiate a key press in both conditions. In this sense, both conditions involved an intentional *when* decision. However, in the veto condition, participants sometimes had to decide to cancel the ongoing action. When looking at the signal changes in the left and right AIC (Fig. 1), it turns out that the AIC activation in the action condition has a value intermediate between the veto condition and the control condition where participants had to judge the onset of a tone. This finding suggests that intentional stopping produces a stronger effect in the AIC than intentional action. Importantly, this rules out simple explanations of the AIC activation in intentional stopping based on reward. In principle, then, the AIC activation in intentional inhibition could correspond to an anticipated reward for action which one nearly obtained. For example, AIC activations were recently reported in relation to both rewards and just-missed rewards (Clark et al. 2009). However, this view would predict strongest AIC activation for actions, with a somewhat lower

Fig. 1 *Upper panel* Brain activation in the anterior ventral insula (*avIns*) for the contrast of intentional inhibition (*veto*) versus intentional action (*act*). *Lower panel* Signal change as a function of veto, act and tone condition in the left and right *avIns*. From Brass and Haggard (2008)



activation for veto, since no reward is actually obtained. Our finding that veto activations exceed action activations show that intentional inhibition has a specific effect on AIC over and above general reward processing.

But how does the veto condition differ from the action condition? In fact, as mentioned above, both conditions involve a decision component. However, the veto condition led to cancellation of the planned behaviour. Hence, the major difference between the conditions does not relate to the decision but rather to the consequences of the decision. We argued that the strong activation in the anterior insula is presumably related to the negative affect or frustration that results from willing an action and then stopping it intentionally. Consistent with this idea, Ramautar et al. (2006) related AIC activation to processing the significance of inhibitory failure. This interpretation would again point to an evaluative role of AIC in intentional action. It is also quite consistent with a recent study that found AIC in relation to disappointment (Chua et al. 2009). Given that the activation was bilateral, however, it is not clear how this fits with the idea that the left AIC is related to positive and the right to negative affect (Craig 2005, 2009).

Interestingly, a second study on vetoing behaviour replicated the dorsal fronto-medial activation but not the activation in the AIC (Kuhn et al. 2009). In this study, participants could stop a ball that was rolling down a ramp from crashing by pressing a key. However, in 50% of the choice condition, they should decide to inhibit the action that prevents the ball from crashing. When contrasting the intentional inhibition trials with the intentional action trials, we found again activation in the fronto-medial cortex.

However, no activation was found in AIC. This result is very surprising given that the AIC was the most prominent activation in the previous study on intentional inhibition (Brass and Haggard 2007). The main difference between the two studies is the effort participants put into the action that they had to stop. In Brass and Haggard (2007), they had to stop an action that they intentionally chose in the first place. By contrast, in the ramp study (Kuhn et al. 2009) they had to stop an action that was triggered by the external signal of the ball rolling downwards.

Another intentional stopping study that yielded AIC activation was carried out in the area of gambling (Campbell-Meiklejohn et al. 2008). A very strong behavioural tendency of pathological and non-pathological gamblers is to continue gambling to recover losses (loss-chasing). In an fMRI study, Campbell-Meiklejohn et al. (2008) demonstrated that the decision to quit loss-chasing is related to fronto-medial cortex activation, and also to AIC activation (MNI: left, $x: -30, y: 20, z: 4$; right, $x: -36, y: 18, z: 0$). This study again found activation in AIC when a highly motivated behaviour had to be cancelled. Finally, a study by Kuhn and Brass (2009) found activation in AIC. In this study, participants had to carry out a choice reaction time task by responding with a left or right key to a letter that was presented on the screen. However, in a small proportion of trials, the letter changed the colour to red in which case participants had to stop the ongoing response. In other trials, it changed the colour to blue in which case participants had to decide whether to stop the action or to execute the action. When comparing the decide trials with the instructed stop trials, activation was found in the left

and right ventral AIC (MNI: left, x : -39, y : 21, z : -7, right, x : 42, y : 25, z : -4). However, activation in the intentional stopping and intentional action condition did not differ. Like in the experiment of Kuhn et al. (2009), the action that participants had to stop was not very effortful. This might explain why intentional stopping did not produce stronger AIC activation.

Taken together, the few studies that investigated intentional stopping found relatively strong evidence for an involvement of the AIC. However, AIC was involved in intentional stopping seems to depend on the effort that participants invested in the to-be-stopped action. It seems that AIC is more strongly activated when inhibiting an action deliberately and effortfully chosen. As the personal impact of the action, or strength of action-tendency (Ach 1905) increases, stopping may itself become more effortful, and have more marked affective consequences.

The role of the AIC in intentional action

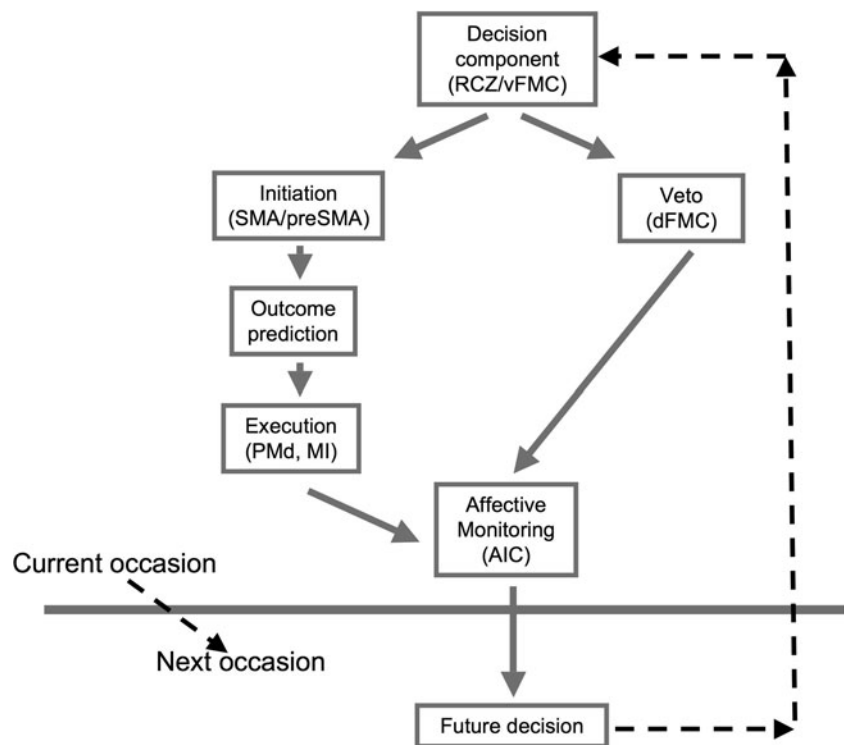
The role of the AIC in intentional action has been widely underestimated. We think that this lack of attention has a number of reasons. First, intentional action is considered to deal with cold cognition. Here a brain area that seems to play a major role in interoceptive aspects of feelings does not fit. In addition, there are methodological problems with identifying AIC activation. Some studies on intentional action focus on specific a priori defined brain areas and do not report brain activation in other areas (Lau et al. 2006). Furthermore, activation in the AIC very often extends into the inferior frontal gyrus and therefore is difficult to identify. However, despite these methodological problems there is clear evidence for the involvement of AIC in intentional action. We reported studies related to all aspects of intention behaviour (when, what and whether) that revealed AIC activation.

How do these results from intentional action fit with the dominant view that the AIC plays a role in interoception (Critchley et al. 2004; Craig 2009)? We suggest that AIC may signal the affective consequences of decisions about intentional action. Voluntary actions are rarely performed in a completely feedforward mode. Rather, the brain monitors action-outcomes to signal whether the action was successful or not. To date, most work on action monitoring has focussed on two key computational problems. The first problem focuses on how the brain determines whether a given sensory signal is a consequence of one's own action, or an action-independent change in the external environment (Blakemore et al. 1998). The second problem focuses on using predicted and sensed information about action execution to rapidly adjust actions (Paulignan et al. 1991). In addition to these 'cold' and real-time forms of action

monitoring for action control, an evaluative, appetitive signal relating to action-outcome may also be important. This signal would not be concerned with controlling the current action, but rather with coding the desirability or undesirability of that action given overall goals. The interoceptive signals elaborated in the anterior insula may play a key role in reinforcing action representations to make them more or less available in *future* situations. That is, the AIC activation in intentional action may correspond to the "feeling of what I made happen", and will be used to train the will for future intentional actions. Humans have a much greater capacity for intentional action than any other species. Moreover, intentional actions are thought to depend more strongly on effect learning than externally-triggered actions (Herwig et al. 2007). Humans, therefore, have a range of flexibility and creativity in their intentional actions which is a profound evolutionary advantage. However, this augmented 'will' would be merely wanton, undirected and useless without an evaluative signal to reinforce which intentional actions are truly valuable, and which are not. Indeed, volition without strong affective constraints may be dangerous, as in psychopathy. We suggest that interoceptive signals in the insula play an essential role in evaluating the consequences of intentional action, and thus in adaptive, affective training of the will. A schematic representation of the possible functional components of this process is shown in Fig. 2.

Several lines of evidence point to this evaluative role for the AIC in intentional action. First, the apparent slow conduction of somatic signals to the insula (Olausson et al. 2010) is consistent with the role in affective guidance of future actions, rather than control of present actions. Second, the evaluative function of the anterior insula is consistent with its role in error awareness (Ullsperger et al. 2010). Third, the activation of AIC when an intentional action is inhibited (see above) could also be related to the learning potential offered by identifying the consequences of not acting, as well as the consequences of acting. Public health officials know, for example, that an effective way to modulate health-related voluntary behaviours is to contrast the consequences of the target behaviour with the consequences of not performing it. Fourth, this view can explain the strong role of conscious experience in intentional action. The build-up of preparatory activity before voluntary action produces a conscious experience of intention just before action itself (Libet et al. 1983; Haggard 2008). However, to be useful for learning, this experience of intention before action needs to be associated with an awareness of the consequences of action after the action is made. For example, if someone has a strong experience of their intention to perform an action, then performs the action and suffers a negative outcome, they may learn to be wary next time they experience a similar intention. This

Fig. 2 A simple functional model of affective monitoring of intentional action in the AIC. A decision to act or inhibit action ('veto') is taken in the prefrontal cortex, perhaps in RCZ or vFMC. Different neural structures are activated depending on the outcome of this decision. Action decisions lead to activation of preSMA and MI, while inhibition decisions lead to activation of dFMC. The affective consequences of either decision are relayed from these areas to the anterior insula (AIC). This affective information is then used to bias decisions either in favour of action or inhibition on subsequent occasions. Since some connections may involve a subcortical loop, in addition to a direct cortical route, the arrows indicate functional flow of information, rather than neuroanatomical connections



would also be consistent with the idea that the strength of anterior insula activation in intentional action depends on the degree of voluntary involvement or effort. The more one is voluntarily involved in an action the more important becomes the evaluation of the sensory consequences. Indeed, there is good evidence that intentional and outcome signals are dynamically integrated in the brain to produce a coherent experience of action (Lau et al. 2007; Moore and Haggard 2008). Frontal circuits generate both voluntary action and the experience of volition (Fried et al. 1991). These action circuits might in turn be linked to insular circuits that provide fundamental somatic signals with clear reinforcement and punishment value. The linkage between action and outcome circuits would ensure that the flexibility and power of volition can be constrained and focussed on beneficial behaviours, rather than destructive or random ones. Phasic dopamine signals may play an important role in making these associations, while providing an intense experience of action and outcome (Redgrave et al. 2008).

Finally, the insular role in marking the outcomes of intentional action is consistent with its reported involvement in anosognosia (Karnath et al. 2005; Karnath and Baier 2010). On one influential view, the anosognosic patient perceives only their intention to move (Berti et al. 2005), and fails to register the somatic signals that they have not in fact moved. In our scheme, insular damage might prevent them from learning that their volition is much less effective after stroke than it was before. This

view would explain why anosognosic patients fail to represent cognitively what they actually could do in a hypothetical situation, as well as failing to perceive what actually occurs when they attempt to move. It may also explain why anosognosia generally resists contrary evidence, such as viewing the static limb (Fotopoulou et al. 2009). However, some caution is needed, since the apparent focus of the anosognosic lesion is in the mid-insula, while the MRI evidence reviewed above suggests that somatic evaluation of intentional action-outcomes involves the anterior insula.

We end with some issues for future research. First, it remains unclear whether insular activation corresponds to an anticipation of action-outcomes, or an afferent signal from the body. fMRI lacks the time resolution to answer this question. Thus, methods with better time resolution will be required to understand the time course of insular activation in voluntary control. Direct epicortical recording from neurosurgical patients with insular epileptic foci may offer one important way forward. Second, difficulties in control of voluntary behaviour should be associated with abnormalities or deficits in insular function. AIC volume has been associated with psychopathy (de Oliveira-Souza et al. 2008; Tiihonen et al. 2008), and with conduct disorder (Sterzer et al. 2007). However, a further recent study on pre-teen boys with conduct disorder found no structural difference in AIC relative to a control group (De Brito et al. 2009). King-Casas et al. (2008) explained impaired co-operation of patients with Borderline Personality Disorder

in a trust game in terms of anterior insula activation. Whereas activation in healthy controls correlated with the trust placed in the player by the opponent, this correlation was less evident in the patients, suggesting a failure to correctly process the social signals upon which appropriate social action is based. A final question concerns whether the AIC is concerned more with reinforcement of intentional action tendencies by positive somatic consequences or punishment by negative consequences. The current fMRI literature reports AIC activations related to both positive reward and to regret. It therefore remains unclear whether the AIC would primarily condition the will appetitively or aversively.

Conclusions

In conclusion, the capacity for voluntary action is perhaps the pre-eminent feature of the human mind and brain. We have argued that, to be useful, voluntary action needs to be tightly linked to a mechanism that evaluates the consequences of voluntary actions. This mechanism would be concerned less with decision about and control over the current action, than with learning the results of current actions in order to predictively guide future action decisions: i.e., constraining the will. The evolutionary development of the human brain's capacity for voluntary action is closely associated with larger social networks. These in turn bring a need for neurobiological and also cultural mechanisms for evaluating voluntary action-outcomes, and thus training the will. We tentatively suggest that the anterior insula cortex houses this mechanism for evaluating intentional action-outcomes. Nietzsche famously thought of human nature as dominated by a will to power, with pleasure and pain being mere secondary epiphenomena. Our view could not disagree more! The coupling of frontal intentional action systems with somatosensory affective systems in action-outcome learning plays an essential role in making volition effective rather than 'blind'. The basis of focussing the capacity for human volition onto initiating productive and creative behaviours may lie in the AIC.

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