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VOLITION

Imaging volition: what the brain can tell us about the will

Marcel Brass · Margaret T. Lynn · Jelle Demanet · Davide Rigoni

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Abstract The question of how we can voluntarily control our behaviour dates back to the beginnings of scientific psychology. Currently, there are two empirical research disciplines tackling human volition: cognitive neuroscience and social psychology. To date, there is little interaction between the two disciplines in terms of the investigation of human volition. The aim of the current article is to highlight recent brain imaging work on human volition and to relate social psychological concepts of volition to the functional neuroanatomy of intentional action. A host of studies indicate that the medial prefrontal cortex plays a crucial role in voluntary action. Accordingly, we postulate that social psychological concepts of volition can be investigated using neuroimaging techniques, and propose that by developing a social cognitive neuroscience of human volition, we may gain a deeper understanding of this fascinating and complex aspect of the human mind.

Keywords Volition · Intentional control · Medial prefrontal cortex · fMRI

Introduction

We each have an intuitive notion of the concept of will, reflected in everyday expressions such as 'where there's a will, there's a way.' Scientifically, the question of how we can voluntarily control our behaviour has fascinated researchers throughout time and across disciplines such as philosophy, psychology, and neuroscience. This question is fundamental to what it means to be human, and is tightly related to socially relevant issues such as responsibility and self-control. The interest surrounding willed behaviour is to some degree fuelled by the old philosophical problem of whether free will exists or not (Kane 1996). And yet this problem, seemingly outside the scope of empirical research (e.g. Roskies 2010), paralysed experimental approaches to voluntary action for many years and prevented (with a few exceptions) the development of paradigms suitable for investigating human volition. Only recently have researchers in the aforementioned fields come to realize that it might be useful to investigate willed behaviour without trying to determine whether free will exists or not (Lau et al. 2004a; Baumeister 2008; Mele 2009).

Volition as a concept is difficult to define and has to be distinguished from related concepts such as motivation and cognitive control. While motivation addresses *why* one strives towards certain goals, volition is related to the mechanisms used in the formation, maintenance, and implementation of goals and intentions (Heckhausen 2007). Furthermore, volition refers to the intentional side of behavioural control, while cognitive control is an overarching concept implicating intentional and contextual aspects of behavioural control. Stopping in front of a red traffic light, for example, has a contextual component, namely the red traffic light inducing me to push the brake and an intentional component, namely me complying with this automatic tendency to push the brake.

In psychology, research on volition has a long-standing tradition (e.g. James 1890). Volition as a psychological concept, however, lost its credibility with the onset of behaviourism and is still not completely rehabilitated, due in part

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M. Brass (✉) · M. T. Lynn · J. Demanet · D. Rigoni
Department of Experimental Psychology, Ghent University,
Henri-Dunantlaan 2, 9000 Ghent, Belgium
e-mail: marcel.brass@ugent.be

M. Brass
Behavioural Science Institute, Radboud University,
Nijmegen, The Netherlands

to the deep scepticism held by experimental psychology against introspection. However, investigating the intentional side of behaviour seems to necessarily rely on phenomenological aspects (Brass and Haggard 2008; Pacherie 2008); volition is strongly defined by its first-person ontology (Searle 2004), that is, the subjective experience of willing something. But can a neuroscience of volition rely on such subjective experiences? The development of brain imaging techniques such as functional MRI has provided a unique opportunity to overcome this scepticism, by allowing the relation of introspective data to objective measurements (e.g. Mason et al. 2007).

Currently, there are two empirical research disciplines tackling volitional behaviour: cognitive neuroscience and social psychology. Starting with the ingenious experiments of Benjamin Libet in the early 1980s (Libet et al. 1983), research on the intentional control of action has focused on the question of whether the conscious experience of will plays a causal role in motor control or is an epiphenomenon. More recently, cognitive neuroscience shifted from the question of free will to the investigation of volition (Brass and Haggard 2008; Haggard 2008) by investigating the dichotomy of intentionally guided action and externally guided action (Jahanshahi et al. 1995; Cunnington et al. 2002; Mueller et al. 2007).

Social psychology, in the meantime, has posed three major questions related to voluntary action: (1) Is our experience of consciously willed behaviour an illusion (Wegner 2002)? (2) To what extent is our behaviour influenced by unconscious sources (e.g. Dijksterhuis et al. 2006)? (3) Is there a capacity of willpower, and if so, how is this capacity modulated by other factors (Baumeister 2008)? While the first question sees the subjective experience of volition as a reconstructive phenomenon, the other two perspectives try to understand the factors that determine volitional behaviour.

The general goal of the present article is to highlight important brain imaging research on human volition. Given the broad scope of the research topic, this article will by no means provide an exhaustive review of the literature. We will address to what extent neuroimaging research contributes to our understanding of the phenomenon, and in doing so attempt to define areas in which further brain imaging investigation might be useful. The first section will focus on cognitive neuroscientific approaches to human volition. We will briefly summarize recent literature that contrasts internally versus externally guided behaviour, and give an overview of studies trying to investigate the subjective side of volition. In the second section, we will review social psychological research by outlining a conception of volition as 'being in control,' then explore research on unconscious determinants of voluntary action and the resource model of willpower. Finally, we will sketch a functional neuroanatomical model of human volition that tries to integrate these diverse perspectives.

Voluntary action as internally guided behaviour

One of the most common ways to conceptualize voluntary action in cognitive neuroscience has been to contrast it with externally guided behaviour (Goldberg 1985). This distinction is based on the idea that actions that are strongly guided by the environment are experienced as less volitional. A simple reflex, for example, does not leave much room for volition. In accordance with this perspective, voluntary action is thus defined as internally guided behaviour, though it must be noted that this conception of intentional action is quite controversial (Nachev and Husain 2010; Passingham et al. 2010; Schuur and Haggard 2011, 2012; Obhi 2012). In particular, it has been argued that the notion of internally guided behaviour is difficult to define operationally, because internal causes of behaviour are not experimentally tractable (Nachev and Husain 2010).

Despite these limitations, a large number of imaging studies (for an overview see Krieghoff et al. 2011) have compared situations in which participants can freely choose to do something (internally guided) with situations in which a stimulus determines the relevant behaviour (externally guided). These studies have indentified an extensive network of brain regions in the medial and lateral frontal cortex, as well as the parietal cortex, as being related to internally guided behaviour (Lau et al. 2006; Krieghoff et al. 2011). Such a comparison, however, involves a number of processes that are not directly related to volition (Passingham et al. 2010). In the free choice scenario, for example, participants are usually instructed not to act in a stereotypic fashion (e.g. to avoid simple alternations between responses), in essence providing an implicit randomness instruction. It has been argued that parts of the fronto-parietal network might be involved in such strategic aspects of the task, by serving to track the sequence of responses across trials in working memory (Lau et al. 2004b). Nevertheless, consensus is evolving that the medial prefrontal cortex (mPFC; see Fig. 1 for the relevant brain regions) is most intimately linked to voluntary action (Brass and Haggard 2008; Passingham et al. 2010). This assertion is supported by the connectivity pattern of the mPFC; while the lateral prefrontal cortex is strongly connected to sensory association cortices providing information about the external world, the mPFC receives interoceptive inputs and is tightly linked to memory retrieval processes involving information about the inner world (Passingham et al. 2010).

More recently, the discussion has focused on the functional relevance of different areas within the mPFC (Lau et al. 2006; Mueller et al. 2007). In particular, two brain

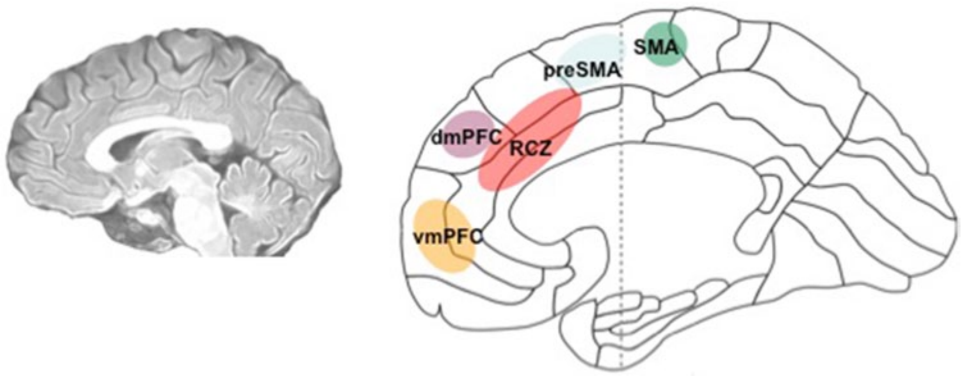

Fig. 1 Brain regions in the medial frontal cortex that have been implicated in human volition. *SMA* supplementary motor area, *preSMA* pre-supplementary motor area, *RCZ* rostral cingulate zone, *dmPFC* dorsomedial prefrontal cortex, *vmPFC* ventromedial prefrontal cortex

regions have been discussed: the rostral cingulate zone (RCZ), a region that extends from the anterior cingulate cortex (ACC) more posteriorly and dorsally (see Fig. 1), and the supplementary and pre-supplementary motor areas (SMA/preSMA). We have recently argued that distinct parts of the medial frontal cortex might be involved in different aspects of intentional action control (Mueller et al. 2007; Brass and Haggard 2008). This was motivated by the observation that intentional action paradigms investigate either decisions between response alternatives (*what* decisions) (Walton et al. 2004; Cunnington et al. 2006; Lau et al. 2006; van Eimeren et al. 2006) or the choice of when to execute a specific predetermined response (*when* decisions) (Libet et al. 1983; Cunnington et al. 2002, 2003). Integrating existing literature (Krieghoff et al. 2011) and our own studies (Mueller et al. 2007; Krieghoff et al. 2009), we argued that the *what* decision is related to the RCZ and the *when* decision to the SMA/preSMA. This perspective is also consistent with the broader functional role of the RCZ in conflict processing (Ridderinkhof et al. 2004). Choosing between response alternatives requires resolving the competition between response options. From this perspective, choice and conflict are two sides of the same coin (Brass and Haggard 2008; Holroyd and Yeung 2012). A very similar perspective has recently been formalized in a computational model (Holroyd and Yeung 2012). Recent neuroimaging work generally supports the distinction of the *when* and the *what* components of intentional action (Hoffstaedter et al. 2013; Momennejad and Haynes 2012). How specific brain regions are mapped on this distinction, however, is an open question that may also depend on the specific paradigm employed (e.g. Hoffstaedter et al. 2013) and the analytic method used (Soon et al. 2008).

While the *when* and *what* of intentional action have been extensively investigated, a third aspect has received less attention in the literature. This latter aspect refers to one's ability to intentionally stop ongoing behaviour (Brass and Haggard 2007, 2008; Filevich et al. 2012). There is a large body of literature on externally triggered stopping that avails itself of paradigms such as the stop signal task (Logan et al. 1984). Internally guided stopping, however, has hardly ever been investigated. In a series of experiments, we were able to show that a specific part of the mPFC, located dorsally and anterior to the RCZ, is involved in intentional stopping and hence in the *whether* component of intentional action (Brass and Haggard 2007, 2008; Filevich et al. 2012). We found this part of the mPFC to be activated when participants chose to stop intentional action (Brass and Haggard 2007) and prepotent behaviour (Kuhn et al. 2009). Furthermore, grey matter density in this brain region was correlated with expressive emotion suppression (Kuhn et al. 2011). This would imply that the mPFC plays a central role in the internal cancellation or inhibition of ongoing action plans.

To conclude, thus far three components of internally guided behaviour have been indentified, namely the *what*,

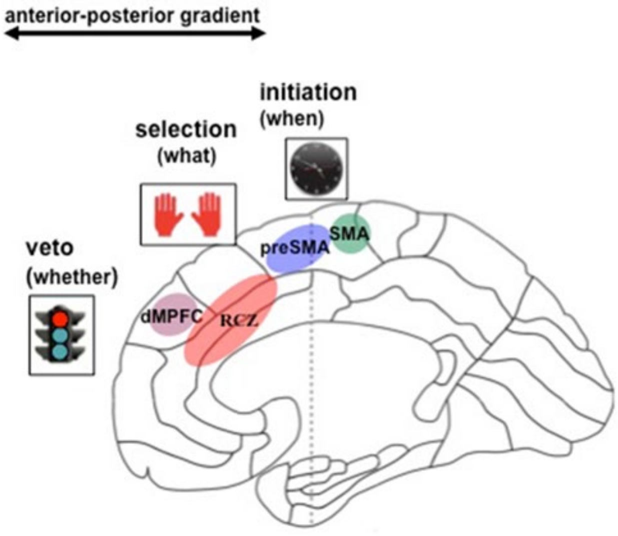

Fig. 2 The WWW model of intentional action and how different components are related to different parts of the mPFC. *SMA* supplementary motor area, *preSMA* pre-supplementary motor area, *RCZ* rostral cingulate zone, *dmPFC* dorsomedial prefrontal cortex, *vmPFC* ventromedial prefrontal cortex

the *when*, and the *whether* components of intentional action. These different components are related to distinct parts of the mPFC. We have recently developed a heuristic functional neuroanatomical model of internally guided behaviour, the so-called WWW model of intentional action (Fig. 2, Brass and Haggard 2008). While this model will form the theoretical basis for the current review, we will try to expand it in a number of respects to provide a more comprehensive framework for intentional action.

The subjective side of volition

The distinction between internally guided and externally guided behaviour is based on objective, third-person criteria, and therefore does not consider the subjective experience of will, that is, its first-person ontology (Searle 2004). This first-person perspective, however, is an integral part of folk psychology surrounding human volition and plays a crucial role in the scientific literature on free will by relating the experience of will to the neural correlates of willful behaviour (e.g. Libet et al. 1983). In accordance with the WWW model of intentional action (Brass and Haggard 2008), this subjective experience can be related to different stages of intentional choice. First, the explicit choice between response options (the *what* component) is related to the subjective experience of making up your mind. There is ‘a sense of alternative choices open to you,’ as Searle put it (Searle 2004, p. 217). Furthermore, choosing between different response options often involves the experience of conflict. The *when* component of intentional action has been related to the experience of *urges*, a feeling of being about to do something (Jackson et al. 2011). Finally, the *whether* component of intentional action is related to disengagement from an action and has been related to the experience of ‘let down’ (Brass and Haggard 2007). It is crucial to point out that the subjective experience of intentional action might strongly depend on the time scale of intentional choice. The subjective experience of choosing which car to buy in the next few months, for example, might completely differ from the choice whether to take a left of a right turn when finding your way in an unknown city.

One fundamental question regarding the first-person ontology of intentional action is whether the same areas that have been identified as being involved in the control of intentional behaviour, through use of objective criteria, are also related to the subjective experience of intentionality (shared circuit view). Addressing this question is onerous because manipulating the subjective experience of will independently from objective variables can be problematic. Furthermore, finding valid and reliable behavioural measures of subjective experiences has proven to be difficult.

Accordingly, there is little neuroscientific research on the first-person ontology of intentional action. One exception is the experience of urges. The concept of an urge is, however, multi-faceted and difficult to investigate (Jackson et al. 2011). First, it is used to describe the bodily sensation of being about to do something (Brass and Haggard 2008). In the Libet task, for example, participants report their time of intention, that is, when they feel the urge to press the key. Here, the urge reflects the subjective component of the intention to act. At the same time, urges have also been related to the experience of sensory events that induce an action (e.g. the tickling of the nose that triggers one to scratch). Finally, urges have been extensively investigated in specific pathologies such as Gilles de la Tourette syndrome (Peterson et al. 1998; Stern et al. 2000; Bohlhalter et al. 2006; Marsh et al. 2007; Mazzone et al. 2010). Importantly, urges primarily occur in situations in which the relevant action is prevented from being executed or is delayed. This makes it very difficult to distinguish the neural correlates of urges from the neural correlates of inhibition of action. Most studies that have investigated urges have focused on the inhibition of automatic responses such as yawning (Jackson et al. 2011) or eye blinking (Chung et al. 2006; Lerner et al. 2009; Berman et al. 2012). These studies consistently identified two brain regions, namely the mPFC and the anterior insula (aINS) (Jackson et al. 2011).

Another way to investigate the subjective experience of intentional behaviour is by directing attention to the relevant representation (Libet et al. 1983). Lau and colleagues (Lau et al. 2004a), for example, asked participants to attend to their intention to act or to the movement itself. Attending to the intention to move led to stronger activation of the preSMA, supporting a shared circuit view.

Interestingly, urges can be induced by intracranial stimulation (Fried et al. 1991; Desmurget et al. 2009). It has been demonstrated that stimulating the SMA/preSMA (Fried et al. 1991), but also the inferior parietal cortex (Desmurget et al. 2009), prompts the urge to do something. This led to the proposal that the posterior parietal cortex (PPC) provides a relatively general movement intention, while motor intentions generated in the SMA/preSMA more closely resemble the specific movement to be executed (Desmurget and Sirigu 2009). These results again seem to support the idea that the experience and control of intentional action might rely on overlapping neural circuits (Desmurget and Sirigu 2009).

To our knowledge, there is hardly any research on the subjective experience of choosing between different response alternatives (the *what* component of intentional action). One notable exception is a recent study in which participants could choose to complete a number series of four digits by adding another digit (Filevich et al. in prep). The first digits were either relatively unsystematic (3121) or highly systematic (1122). At the end of each trial, participants had to indicate how free they felt about the choice. Interestingly, participants felt more freedom to choose a number when the previous numbers where unsystematic compared to the systematic case. When correlating the subjective experience of choice with brain activity, no overlap was found with brain areas involved in intentional choice. These data seem to suggest that brain areas related to the subjective experience of choice are distinct from brain areas involved in the control of intentional choice.

Finally, there is a dearth of systematic research on the subjective experience of the intentional choice not to act. Anecdotal reports suggest that the intentional choice to stop ongoing behaviour is related to a feeling of 'let down,' or disappointment. The aINS has been related to this subjective experience (Brass and Haggard 2007). Such a finding would be consistent with a number of studies on urges in which an automatic or prepotent response has to be inhibited (for an overview see Jackson et al. 2011).

To summarize, there is little neuroscientific research on the first-person ontology of intentional action. Most relevant research has been carried out on the experience of urges, though finding examples of purely volitional urges is problematic. Some recent studies suggest that the SMA/preSMA and PPC are associated with subjective experience stemming from the initiation component of action, supporting the idea that similar brain regions are involved in the control and subjective experience of intentional action. Further research and new paradigms are required to determine the subjective influences upon intentional action.

Volition as being in control

While the previous section dealt with the subjective experiences accompanying intentional behaviour, the current section is related to a more abstract subjective component of intentional action, namely the feeling of being in control over one's own behaviour. From very basic actions (e.g. choosing where to orient one's attention in the visual field) to more complex behaviour (e.g. choosing to stop by a patisserie and buy a cake to celebrate a friend's birthday party), people feel they can choose, at least to some degree. The feeling of being in control is often referred to as the sense of agency (Gallagher 2000). The sense of agency has multiple aspects, ranging from unconscious and pre-reflexive to explicit reflexive processes (Gallagher 2000). In addition, being in control seems to be a biological need and therefore is strongly connected to basic motivational processes.

Research in cognitive neuroscience has focused on two relatively distinct aspects of being in control: the sense of being at the origin of the action (see Decety and Lamm 2007 for a review) and the motivational aspects of being in control (see Leotti et al. 2010 for a review). The former line of research explores the cognitive and neural mechanisms involved when we attribute a motor action to the self, as opposed to another entity, while the latter conceptualizes the sense of control as a biological need, and thus holds one's belief that they are able to exert control over their behaviour as highly adaptive.

A series of experiments demonstrated that two specific brain regions are differentially activated when we perceive ourselves versus other people as the cause of an action. Spence and colleagues (Spence et al. 1997) observed that the right inferior parietal lobe is more active when patients with delusions of control believe that someone else has performed movements that were in fact performed by the patient. In a PET study, Ruby and Decety (2001) showed participants pictures of common tools (e.g. razor, telephone) and asked them to imagine themselves or someone else using the tools. They found increased activation of the right inferior parietal lobe when participants imagined someone else performing the same action as compared to when they imagined themselves using the tool. Conversely, the left aINS was more active when participants assumed the first-person perspective. The same pattern of brain activation was reported in an fMRI study (Farrer and Frith 2002) in which participants were asked to drive a circle through a T-shaped path by using a joystick. Participants were asked to perform the task on each trial, but they were told that the circle could be controlled either by themselves or by the experimenter. In the first condition, participants were therefore aware of being in control of the circle, and this lead to an activation of the aINS. In the latter case, being aware that the circle was directed by the experimenter was associated with activation in the inferior parietal cortex. These results have been confirmed by other studies (Farrer et al. 2003; Spengler et al. 2009) that further specify that the temporo-parietal junction (TPJ) plays a crucial role for the sense of agency in the parietal lobe. For instance, activity over this region increased with greater degrees of subjective discrepancy between predicted and actual action effects (Spengler et al. 2009).

To summarize, there exists evidence from neuroimaging and patient studies indicating that the inferior parietal lobe, and more precisely the TPJ, is involved in the distinction between self-produced and others-produced actions. In addition, awareness that an action originates with the self is associated with increased activity in the aINS.

While these studies show an involvement of the inferior parietal cortex and of the aINS in the sense of agency, other research examines the motivational aspects of being in control and questions why the need to feel as if we are the agents of our own actions is so fundamental to our experience of the world. The essence of this approach is that the sense of being in control is a primary need that is biologically motivated, as it is adaptive for survival (Leotti et al. 2010).

Without the feeling that our behaviour can be controlled and therefore improved, there would be little incentive to make even a minimal effort to face environmental or social challenges. Indirect support for this view comes from recent studies showing that weakening the belief in volitional control can impact social behaviour (Vohs and Schooler 2008b; Baumeister et al. 2009) as well as neural (Rigoni et al. 2011) and cognitive (Rigoni et al. 2012) processes underlying voluntary behaviour. Overall, these studies suggest that self-control (i.e. the effort we expend to regulate our behaviour) depends on whether or not we believe we can exert control over our actions: undermining the notion of being in control will result in more impulsive, automatic, and therefore potentially maladaptive actions.

The need for personal command over behaviour is very strong, and people display a natural tendency to experience control even regarding uncontrollable events. Phenomena such as the illusion of control (Langer 1975), where personal control is perceived when there is no true control over a situation or an event, may be interpreted as protective mechanisms, preventing maladaptive coping. The concept of being in control as a biological need is confirmed by the well-known 'learned helplessness' phenomenon: animals or humans experiencing a lack of control in an uncontrollable situation may display helpless reactions (e.g. depression, maladaptive coping) in the future, even when the situation is controllable (Abramson et al. 1978). Thus, the mere exertion of choice is rewarding in and of itself and reinforces the belief that we are in control (see Shapiro et al. 1996).

Data from cognitive neuroscience support the link between being in control and the reward system. Overall, rewarding outcomes that are delivered dependent upon an individual's behaviour tend to activate regions of the neural reward system to a greater extent than rewards that are independent of the individual's response (O'Doherty et al. 2004; Tricomi et al. 2004; Bjork and Hommer 2007). For instance, in an fMRI study, Tricomi et al. (2004) compared brain activity resulting from rewards and punishments that were either contingent or non-contingent upon participants' actions. Subjects were asked to press a button in response to an anticipatory cue stimulus. In one condition, they were told that they had no control over what feedback (i.e. monetary gain or loss) would follow the cue. In another condition, subjects were told to guess the 'correct' answer (outcomes were actually predetermined), and that whether they won or lost money on these trials would depend on whether they guessed correctly. Results showed increased activity in the striatum when feedback was associated with the 'contingent' condition. It is known that the striatum is involved in reward processing and goal-directed behaviour, and therefore these results are in line with the idea that the possibility of choice is inherently rewarding. In another study (O'Doherty et al. 2003), participants were presented with two stimuli associated with different reward probabilities. In the 'choice' condition, participants could freely choose the stimulus and were then rewarded or punished. In the 'imperative' condition, participants were shown the actual reward or punishment, but they had no active role in the stimulus selection, which was actually selected by the computer. Feedback-related activity in the medial and the central orbitofrontal cortex was enhanced in the choice condition as compared to the imperative condition. Tanaka et al. (2008) recently reported that neural activity in the medial orbitofrontal cortex, mPFC, and dorsal striatum were modulated as a function of action–reward contingency. Neural responses in these regions increased when the presentation of feedback was highly contingent upon participants' responses. Interestingly, they found that the mPFC also correlated with the *subjective* experience of causality (i.e. the degree to which they feel responsible for the outcomes), suggesting that this region may track the subjective sense of being 'at the origin' of the choice. This control-related activity of the mPFC is in line with studies showing that the mPFC is activated to a greater extent when individuals choose between alternatives that are relevant for the self, as compared to when choices are not self-referential (Johnson et al. 2005; Schmitz and Johnson 2007). Taken together, these findings indicate that the prefrontal cortex, in particular the mPFC, and the striatum play a fundamental role in the subjective sense of control. The fact that these regions are anatomically and functionally interconnected (Levy and Dubois 2006) suggests that this corticostriatal circuit may underlie the interaction between reward-related motivational states and the sense of being in control.

The sense of control is a pervasive human experience. Only recently has neuroscience begun to understand the brain regions involved in this subjective experience. On the one hand, a sense of control results from the ability to distinguish between behaviour that originates with the self and behaviour that is generated by others. This 'cognitive' ability involves the parietal cortex, in particular the TPJ, and the aINS. On the other hand, being in control is inherently rewarding, and thus is strongly linked to motivation: we not only feel like the agents of our behaviour, but we perceive situations involving the possibility of choice and control as preferable and more rewarding. Accordingly, the exertion of choice is associated with increased activity of the striatum, a brain region involved in the evaluation of motivationally relevant stimuli, and the mPFC, which is involved in the perception of control. The biological preference for control presumably has its basis in the interaction between the reward- and self-related areas within the corticostriatal network.

The unconscious will: top-down and bottom-up influences on intentional action

Ever since Freud introduced the notion of the unconscious (Freud 1923), it has been a commonplace assumption that our intentional actions are not only the result of explicit deliberation but also the consequence of unconscious processes. Over the last two decades, social psychology has systematically investigated the role of unconscious processes in human choice behaviour (Custers and Aarts 2010; Dijksterhuis and Aarts 2010). There is a minimum of three ways to investigate the role of unconscious processes. First, one can prime a specific concept or action unconsciously, then investigate whether such priming has an influence upon which action is chosen (Schlaghecken and Eimer 2004). Here, the crucial question is whether unconscious information influences behaviour. This priming research has been carried out with relatively abstract social concepts (Dijksterhuis and Bargh 2001; Kay et al. 2004; Holland et al. 2005), but also with low-level constructs such as priming specific response options or tasks (Elsner and Hommel 2001; Schlaghecken and Eimer 2004; Wenke et al. 2010; Reuss et al. 2011). There exists some imaging work on unconscious priming (e.g. Lau and Passingham 2007; De Pesapia et al. 2012), yet the manner in which unconscious priming influences free choices has thus far, to our knowledge, not been investigated.

Second, one can investigate whether unconscious processing of information leads to an improvement of decisions. Here, the question is whether unconscious processing is sometimes more efficient than conscious processing of information. One line of research provides complex problems to participants and then prevents them from deliberating on the problem by introducing a secondary task (Dijksterhuis et al. 2006; Strick et al. 2011). It has been demonstrated that complex decisions sometimes benefit from unconscious information processing. This approach, however, makes it very difficult to determine the brain regions involved in regulating unconscious information, as unconscious processes are masked by a secondary task. Furthermore, the question arises whether unconscious information processing exclusively occurs in the secondary task condition, or whether a kind of perpetual background activity is only prevented from influencing the decision when explicit deliberation overrides it.

Finally, researchers have investigated brain activity preceding intentional choices. This line of inquiry tries to determine to what extent preconscious processes predetermine intentional choice. The classical Libet experiment (Libet et al. 1983) is a prime example of this approach. It showed, for the first time, that the intentional choice to press a key is preceded by a systematic pattern of brain activity, namely the readiness potential. The functional meaning of the readiness potential, however, has been strongly debated over the last 20 years (Hallett 2007). The initial interpretation was that it reflects preconscious motor preparation. However, it was recently proposed that the readiness potential might instead reflect averaging of random noise that exceeds a specific threshold (Schurger et al. 2012).

Recent fMRI studies go beyond the mere demonstration of systematic brain activation preceding intentional choice. These studies try to predict a given choice using pattern classification of brain activity (Soon et al. 2008; Bode et al. 2011). In this way, it is possible to quantify the degree to which a choice can be predicted. Furthermore, it allows for the localization of brain regions carrying predictive information. This research demonstrates that it is possible to predict human decisions seconds before participants themselves become aware of their choices (Soon et al. 2008). The prediction rate, however, is relatively low. This raises the question of whether these early predictive cues are the precursors of intention or rather biasing signals that influence the later choice process (see also Haynes 2011).

Importantly, two of the brain areas that carry early predictive information, namely the anterior medial PFC and retrosplenial cortex, are the central nodes of the so-called default mode network (DMN). The DMN is most consistently observed when participants are not involved in a specific task, and has been related to evaluative (Zysset et al. 2002) and stimulus-independent processes (Mason et al. 2007; Buckner et al. 2008). In the context of intentional choice, these regions might provide a kind of background information that biases choice. We have recently argued that decisions between opposing response options are determined by bottom-up and top-down processes. Top-down processes reflect the task instruction and explicit deliberation, and are implemented in more posterior medial prefrontal brain regions such as the RCZ. Predictive information in the anterior prefrontal cortex and the retrosplenial cortex can bias choice particularly in situations in which the choice is more or less arbitrary. Hence, bottom-up and top-down processes are reciprocally related. The more a choice is influenced by top-down information, the less it is determined by bottom-up information. We tested this hypothesis by introducing a bias to choose one over the other alternative. Our data show that the more a choice was biased the less activation was found in the RCZ (Demanet et al. 2013).

Interestingly, the most anterior part of the prefrontal cortex has also been related to delayed intentions. Often we form intentions that are directed to the future. The degree to which these intentions are specified determines how likely it is that we implement them later on (Gollwitzer 1999). A few recent brain imaging studies have investigated delayed intentions (Gilbert et al. 2009; Gilbert 2011; Momennejad and Haynes 2012) and indicate that they are processed in the most anterior part of the prefrontal cortex, namely the frontopolar cortex. This finding is consistent with research on the maintenance of specific task goals while simultaneously working on a secondary task (so-called branching; Koechlin et al. 1999). Whether delayed intentions are represented in the frontopolar cortex, or whether this region controls the representation of delayed intentions in posterior brain regions remains a matter of debate (Gilbert 2011; Momennejad and Haynes 2012). Furthermore, it is an open question whether brain regions involved in the processing of delayed intentions overlap with brain regions from which future decisions can be predicted before participants become aware of their decisions.

Volition as a limited resource

A dominant social psychological perspective regarding human volition views the human will as a capacity fuelled by a common limited resource, or willpower (Baumeister et al. 1998; Baumeister 2003; Vohs et al. 2008; Vohs and Schooler 2008a). Tasks considered to require willpower include self-control, decision-making, complex problem solving, and conflict resolution. From this perspective, there is not one task that depletes the human will, but rather a number of tasks that draw more or less on this resource. In a series of behavioural studies, Baumeister and colleagues showed that differing tasks presumed to rely on willpower indeed systematically interfered with each other (Baumeister et al. 1998; Muraven and Baumeister 2000; Baumeister 2003). More specifically, they demonstrated that carrying out a task that strongly relies on willpower leads to a depletion of this resource (so-called ego depletion), and results in impaired performance in subsequent tasks also relying on willpower (Baumeister 2003; Vohs et al. 2008). Carrying out a self-control task, for instance, tends to lead to reduced persistence at a difficult problem-solving task. Furthermore, making free choices to perform attitude-relevant behaviour leads to a similar reduction for the following task. A second basic assumption of the willpower metaphor is that willed behaviour is very effortful and therefore requires more energy than behaviour that does not rely on willpower (Gailliot and Baumeister 2007; Gailliot et al. 2007). Support for the idea of higher-energy requirements for processes involving willpower stems from the observation that such processes are very sensitive to one’s neural glucose level (Gailliot and Baumeister 2007). The central notion of the willpower metaphor as a limited resource has recently been called into question. Job and colleagues (Job et al. 2010) demonstrated that manipulating beliefs about the veracity of the limited-resource theory was sufficient to influence the effectiveness of ego depletion. Similarly, Clarkson et al. (2010) found that regardless of how depleted participants *actually* were, if they perceived themselves as less depleted, they failed to demonstrate ego depletion effects during subsequent task performance. A recent study showed that reminding participants of money counteracted ego depletion effects, presumably by reducing the subjective experience of effort or difficulty (Boucher and Kofos 2012). Finally, Beedie and Lane (2011) questioned the idea that limited supply in glucose might be responsible for a resource limitation of willpower. They assert that willpower is not a limited resource but rather refers to a regulatory mechanism that determines how much effort someone invests in a specific task.

But how plausible is the idea of a common resource of willpower from a cognitive neuroscience perspective? Moreover, can such an idea be tested using neuroscientific methods? From a functional neuroanatomical perspective, the idea of a common resource that fuels willed action is quite appealing and leads to predictions that are easily testable. The most straightforward prediction is that willpower relies on a common set of brain regions. Interestingly, most of the tasks that are described as drawing on willpower are tasks that involve the mPFC, and in particular the ACC. As outlined above, we could show, for example, that self-control in a simple motor task involves the mPFC (Brass and Haggard 2007; Kuhn et al. 2009). Furthermore, there is converging evidence that intentional choice primarily draws on the RCZ (Mueller et al. 2007; Krieghoff et al. 2009). In addition, there are a multitude of studies showing that the ACC is involved in conflict tasks (Ridderinkhof et al. 2004). The idea that willed behaviour is more effortful than automatic or stimulus-guided behaviour is also indirectly supported by brain imaging studies on intentional action. When comparing intentional decisions with environmentally guided behaviour, one usually finds strong activations for intentional decisions but no or only minor activations for the reversed contrast (e.g. Mueller et al. 2007). Brain imaging research in support of the ego depletion concept, however, is scarce. In a recent study, Wagner and Heatherton (2012) could show that effortful intentional control led to increased activity in the amygdala in response to negative scenes. Furthermore, functional connectivity between the amygdala and anterior ventromedial prefrontal cortex was reduced in the ego-depleted group.

The research outlined here suggests that the mPFC, and in particular the ACC, might be a central node in the neural circuit related to willpower. From what we know about the ACC, however, it is not plausible to assume that it provides a common resource, but rather that it has a kind of regulatory function determining the level of effort that is invested in a task (Holroyd and Yeung 2012). In a recent position paper, Holroyd and Yeung (2012) argued that the ACC is involved in choosing between different behavioural options and determining the level of effort that is invested in executing the chosen behavioural option. This description is consistent with the idea that the ACC implements a regulatory mechanism that determines the intentional investment in a specific response option or task. Accordingly, there is strong evidence for construing willpower as a regulatory function that can be related to specific brain structures in the mPFC. While such a regulatory mechanism is evidently required in situations of self-control and complex choice, we argue that any kind of intentional decision draws to some degree on this mechanism.

The funnel model of intentional action

Based on the research outlined above, we propose an extension of the WWW model of intentional action. This extension assumes that intentional action follows a kind of funnel-like organization that is related to an anterior-posterior gradient within the medial frontal cortex. It is, however, crucial to note that while this model focuses on the role of the mPFC in intentional action, we assume that areas in the lateral prefrontal cortex, subcortical regions, and parietal regions are involved in intentional control of action as well.

Our model assumes that early stages of intentional action are related to anterior prefrontal brain regions. These brain regions process complex and heterogeneous information that is only broadly determined by specific task instructions or goals. Processing in these brain regions provide a sort of informational background, or intuition, and has a biasing function towards later processing stages. This complex set of information is funnelled when information travels more posteriorly and enters later stages of intentional action. Regions in the RCZ are related to choices between different response options. Such choices are biased by bottom-up information but also by concrete instructions that operate as a top-down influence and thus are a result of the interplay between top-down and bottom-up processing. Furthermore, the RCZ determines the level of effort that is invested in pursuing a specific behaviour and thus regulates the 'willpower' that is invested in a specific choice. When a specific response option is selected, this information is transferred to brain areas more closely related to the motor system, namely SMA/PreSMA. Here, the impulse to initiate a specific response is generated. At this point in the processing stream, it is still possible to disengage from the intention to act (Brass and Haggard 2007) or to change the intended behaviour (Obhi et al. 2009). Intentional inhibition is achieved by a signal from the dorsomedial prefrontal cortex that downregulates activation in the SMA/preSMA (Kuhn et al. 2009). As a working hypothesis, we assume that the subjective experience of volition results from supra-threshold activation in brain circuits that are involved in the control of intentional action. Such subjective experiences are phenomenologically rich because they can be related to any level of the processing stream, ranging from intuitive feelings to concrete urges to act.

The funnel-like organization of human volition guarantees that choices are based on a broad scope of information. At the same time, it also ensures that we can choose very quickly and efficiently when necessary. Whether our choices are primarily determined by intuitions and introspective thoughts, or by explicit deliberation and task instructions, strongly depends on the specific task context and the time frame of our choices.

Open questions

In describing the functional neuroanatomy of human volition, we have attempted to develop a conceptual framework that integrates existing cognitive neuroscientific research and social psychological research on volition. This approach, however, does not address a number of important issues related to voluntary action. While we have concentrated on the role of the mPFC in human volition, it is obvious that this part of the brain does not operate in isolation. As outlined above, the parietal cortex plays an important role (Desmurget and Sirigu 2009), as does the anterior insular cortex (Brass and Haggard 2010). The aINS is often co-activated with the ACC. It seems to play a crucial role in awareness of internally originating information, so-called interoceptive awareness (Craig 2009). Like the ACC, this brain region is extremely sensitive to the effort that is invested in a specific activity. Another open question is related to the interaction between medial prefrontal and lateral prefrontal brain regions in intentional action. We assume that the mPFC is involved in intentional control, and the lateral PFC in contextual control of behaviour, yet intentional control of action necessarily relies to some degree on contextual factors. Furthermore, it is difficult to imagine any cognitive control scenario that lacks an intentional control aspect. Finally, when investigating intentional control in the laboratory, task instructions invariably play a crucial role. The experimenter determines the confines of what participants are allowed to intend, and which choices they are permitted to make. Recent brain imaging research has revealed the neural circuits involved in the implementation of verbal instructions (Ruge and Wolfensteller 2010; Hartstra et al. 2011, 2012). How these brain circuits interact with circuits involved in intentional action is an open question. Finally, laboratory research on human volition does not have a high ecological validity. Neuroscientific research on voluntary action usually investigates choices between arbitrary response options. In our daily life, however, we usually chose between alternatives that have a specific value or lead to specific consequences. Integrating cognitive neuroscience research on human volition with social psychological research might help to overcome this lack of ecological validity.

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