

Human volition: towards a neuroscience of will

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Abstract | The capacity for voluntary action is seen as essential to human nature. Yet neuroscience and behaviourist psychology have traditionally dismissed the topic as unscientific, perhaps because the mechanisms that cause actions have long been unclear. However, new research has identified networks of brain areas, including the pre-supplementary motor area, the anterior prefrontal cortex and the parietal cortex, that underlie voluntary action. These areas generate information for forthcoming actions, and also cause the distinctive conscious experience of intending to act and then controlling one's own actions. Volition consists of a series of decisions regarding whether to act, what action to perform and when to perform it. Neuroscientific accounts of voluntary action may inform debates about the nature of individual responsibility.

Most adult humans have a strong feeling of voluntary control over their actions, and of acting 'as they choose'. The capacity for voluntary action is so fundamental to our existence that social constraints on it, such as imprisonment and prohibition of certain actions, are carefully justified and heavily regulated. Equally, disorders of voluntary action, such as abulia or psychosis, are features of many psychiatric and neurological conditions¹. Despite this importance, it is difficult to provide a satisfactory account of what makes a particular action voluntary. A dualistic view of endogenous causation is engrained in our normal language. Everyday language suggests that 'I' consciously choose to perform actions and that 'my' choice somehow causes the action to occur. This language is dualistic, as it implies a mental 'I' that is distinct from both the brain and the body but that can nevertheless trigger brain events and, thus, bodily movement². A scientifically more satisfactory approach defines voluntary action by contrasting it with stimulus-driven actions: voluntary action lies at one end of a continuum that has simple reflexes at the other end. Thus, whereas reflexes are immediate motor responses, the form of which is determined by the form of stimulation, the occurrence, timing and form of a voluntary action are not directly determined, or at best are only very indirectly determined, by any identifiable external stimulus. Voluntary actions thus demonstrate a 'freedom from immediacy', to use a phrase coined by Shadlen³. This stimulus-independence makes voluntary actions hard to study experimentally.

This Review first describes some of the issues that are involved in measuring volition. It then considers the

brain circuits that are involved in voluntary action, and outlines a view of voluntary action that is based on how these circuits could make decisions in situations in which actions are under-determined. Finally, it considers the relations between voluntary action and consciousness.

Measuring volition

Experimental studies generally deliver a known input or stimulus to a system and measure the system's response. However, this approach is incompatible with the concept of voluntary action being stimulus-independent. To resolve this problem, most experimental studies have given a stimulus or instruction that only partly determines what a participant should do, in one of three ways: the participant performs a fixed action but chooses when to do so⁴; the participant performs an action at a specified time but chooses which of a number of actions to perform^{3,5,6}; or the participant chooses whether or not to perform an action^{4,7,8}. Most studies can be criticized for failing to capture the context of natural human volition: in particular, there is in these studies generally no reason or value that motivates the participant to choose one action over another. In addition, instructing a person to be voluntary is rather paradoxical. However, such studies do capture a key computational feature of voluntary action, namely that the participant must themselves generate the information that is needed to perform an action. A recent radical view effectively dismisses 'voluntariness' as a socially constructed artefact of the experimental situation rather than a genuine cognitive process⁹. From this view, the typical instructions in voluntary-action studies effectively invite

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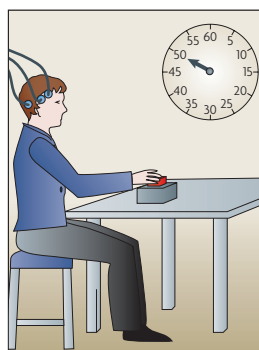
participants to behave in a way that reflects their understanding of 'free will'. Participants might interpret this as a requirement for randomness over trials, leading them to monitor their own performance and selectively vary it¹⁰. However, these criticisms focus on repeated, iterative choice and do not undermine the concept of generating information for an occasional, individual action.

Contrasting voluntary actions with reflex actions provides several useful neuroscientific pointers. Voluntary actions involve the cerebral cortex, whereas some reflexes are purely spinal. Volition matures late in individual development, whereas reflexes can be present at or before birth. Finally, voluntary actions involve two

distinct subjective experiences that are generally absent from reflexes. These are the experience of 'intention' — that is, planning to do or being about to do something — and the experience of agency, which is the later feeling that one's action has indeed caused a particular external event¹¹. For example, a person who switches on a light might experience the intention to perform the action at a particular moment¹² (BOX 1). When the light goes on, the person attributes this change to their action and so experiences confirmation that they caused this external event. By contrast, when a physically similar movement is evoked by a reflex, such as in a knee jerk, the experiences of intention and of control are both absent.

Box 1 | Measuring conscious intention

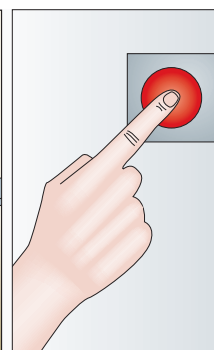
1 Observe clock



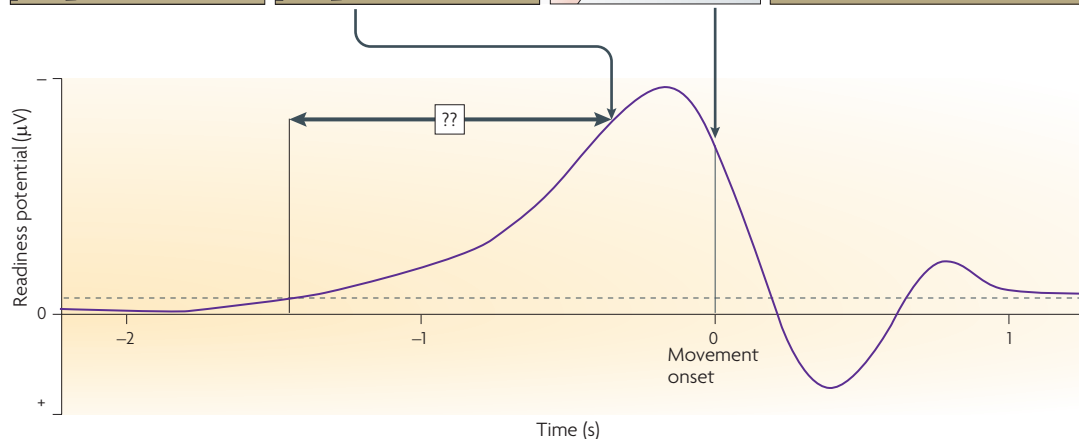
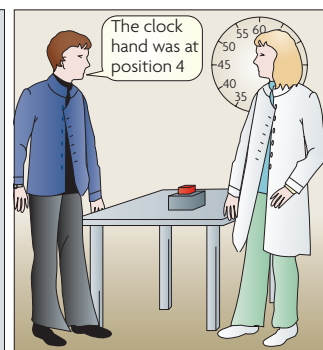
2 Note clock position at time of conscious intention (urge to act)



3 Perform action



4 Report clock position at time of conscious intention



Libet⁴ described an experiment that seems to disprove the everyday concept of 'free will' (see figure). The method is an adaptation of Wundt's classical technique⁹⁶. Participants watch a spot or clock hand rotating on a screen. At a time of their own choosing they spontaneously make a movement of the right hand. The clock stops after a random interval, and the participant reports the position of the clock hand at the moment when they first 'felt the urge' to move their hand. At the same time, electrodes placed on the scalp record the activity of prefrontal motor areas in preparing the movement. A schematic 'readiness potential' recorded in this way is shown in the figure. On average, participants reported the conscious intention to act 206 ms before the onset of muscle activity. By contrast, preparatory brain activity could begin 1 s or more before movement. Therefore, the brain clearly prepared the action over a considerable period before the participant became aware of the intention to act.

Libet's experiment has been widely discussed and extensively criticized, but also replicated^{6,93,97,98}. One objection is that the real voluntary action is the participant's decision to join the experiment in the first place, and that it is the processes associated with this action, rather than the feeling of being about to move, that provides the experimental data. Other objections emphasize that subjective estimates of when conscious experiences occur are unreliable; for example, results may vary according to how the participant divides attention between the clock and their own motor preparation. Indeed, the brain frequently manufactures conscious experiences after the event, retro-inserting them into the stream of consciousness.

A continuum between reflexes and voluntary actions would require intermediate cases. Humans and other animals readily learn to associate motor responses with arbitrary sensory stimuli, such as green and red lights respectively signalling 'go' and 'stop'. When a person starts crossing a road in response to a green signal, the timing and form of their action is related to the stimulus. On the other hand, the action might not occur every time the stimulus occurs. Specifically, its occurrence depends on whether the person wants to cross the road, and perhaps on whether the person has some reason to do so. Therefore, responses to external stimuli usually have features of both reflex actions and voluntary actions.

The development of the association cortex in recent evolution has allowed motor responses to link to stimuli not only directly, as in object-oriented actions like grasping, but also arbitrarily, flexibly and conditionally⁵. 'Voluntary actions' could simply refer to the limiting case of particularly intelligent responses to situations and contexts. However, the view that voluntary actions are in some sense special is supported by evidence for distinct neural pathways associated with voluntary action and stimulus-driven action, as discussed in the next section.

Brain circuits for voluntary action

The human and primate brain both contain several distinct cortical motor circuits that contribute to voluntary action (FIG. 1). These circuits converge on the primary motor cortex (M1), which executes motor commands by transmitting them to the spinal cord and muscles. M1 was therefore considered to be a 'final common path' (REF. 13) for voluntary action. It receives two broad classes of inputs, which subserve voluntary and stimulus-driven actions, respectively¹⁰⁵. More recent work suggests that other cortical motor areas also send outputs to the spinal cord. However, many of these show similar preferences for voluntary and stimulus-driven actions, suggesting that there is a fundamental distinction in the cortical organization of action¹⁴.

One key input reaches M1 from the pre-supplementary motor area (preSMA), which in turn receives inputs from the basal ganglia and the pre-frontal cortex¹⁵ (FIG. 1a). Several human-neuroimaging studies compared the brain activity for manual actions performed at a time of the participant's choice with that for similar actions performed in response to an external stimulus^{16,17}. These showed stronger activation of the preSMA for self-paced actions than for externally triggered actions. The preSMA forms part of a wider frontal cognitive-motor network that includes the premotor¹⁸, the cingulate¹⁴ and the frontopolar cortices. The role of the preSMA is confirmed by recordings from scalp electrodes, which show a prolonged and increasing negativity that begins 1 s or more before the onset of voluntary movement^{19,20}. The source of the early part of this 'readiness potential' has been localized to the preSMA^{20–22}. The onset of the readiness potential is often seen as the initiation of a cascade of neural activity that spreads from the preSMA back to the SMA proper and M1, thus causing movement (FIG. 1b). However, this view has methodological

and theoretical difficulties. First, readiness potentials are measured as voltage increases relative to a neutral baseline period before the activity of interest. In stimulus-locked recordings the baseline is normally taken just before stimulus delivery. But what would be the correct baseline before a voluntary action? This is an important question, because deciding on a baseline presupposes that one knows when the neural precursors of action begin. In practice, preparatory brain activity may begin as early as researchers are able to look for it. For example, recent attempts to decode free choices using new algorithms suggest that neural preparation begins much earlier than was previously thought²³. Second, the preparatory activity of the preSMA must itself be caused. The brain's circuits for voluntary action might consist of loops rather than linear chains that run back to an unspecified and uncaused cause (the 'will'). Indeed, the input from the basal ganglia to the preSMA²⁴ is thought to play a major part in the initiation of action. For example, patients with Parkinson's disease, in whom the output from the basal ganglia to the preSMA is reduced, show less frequent and slower actions than healthy controls²⁵. Moreover, signals that predict a forthcoming voluntary response can be recorded some 2 s before movement onset from electrodes implanted in the basal ganglia — these signals thus precede the typical onset time of readiness potentials²⁶. The subcortical loop through the basal ganglia integrates a wide range of cortical signals to drive currently appropriate actions, whereas dopaminergic inputs from the substantia nigra to the striatum provide the possibility to modulate this drive according to patterns of reward²⁷. From this view, voluntary action is better characterized as a flexible and intelligent interaction with the animal's current and historical context²⁸ than as an uncaused initiation of action. The basal ganglia–preSMA circuit has a key role in this process.

By contrast, a second cortical network that converges on M1 plays a part in immediate sensory guidance of actions (FIG. 1a). Information from early sensory cortices is relayed to intermediate-level representations in the parietal lobe and thence to the lateral part of the premotor cortex, which projects in turn to M1²⁹. This parietal–premotor circuit guides object-oriented actions, such as grasping, using current sensory input. Delays of as little as 1 s between stimulus presentation and motor response result in a switch away from this 'dorsal' route towards other circuits³⁰. However, recent studies suggest that this circuit also contributes to some aspects of 'voluntary' behaviour. For example, single-unit recordings from the primate intraparietal sulcus in tasks in which the animal must choose between equally rewarding alternatives show that neurons in the lateral intraparietal area (LIP) might encode the specific behavioural outcome that the animal has chosen^{31,32}. Thus, when immediate action is required, the parietal–premotor circuit might arbitrate between action alternatives whereas, in the absence of immediate instruction, the basal ganglia–preSMA circuit might be more involved in initiating actions. The two circuits could thus implement different kinds of decisions, both of which are relevant to human volition.

Voluntary action as decision making

The introduction described how everyday language views voluntary action as a moment of endogenous mental choice. In fact, volition is better described as a set of processes in the specific brain circuits described above (FIG. 2). These processes jointly specify several kinds of information that determine our actions, so voluntary action is therefore a form of decision making. Decisions

about action differ from perceptual decisions in several ways. Action decisions such as ‘Should I do something?’ and ‘How should I do it?’ are typically ill-posed, in the sense that they allow several possible solutions. Many perceptual decisions, by contrast, involve reducing complex stimulus information to simpler descriptions. The motor brain must generate new information to make action decisions, whereas the perceptual brain needs

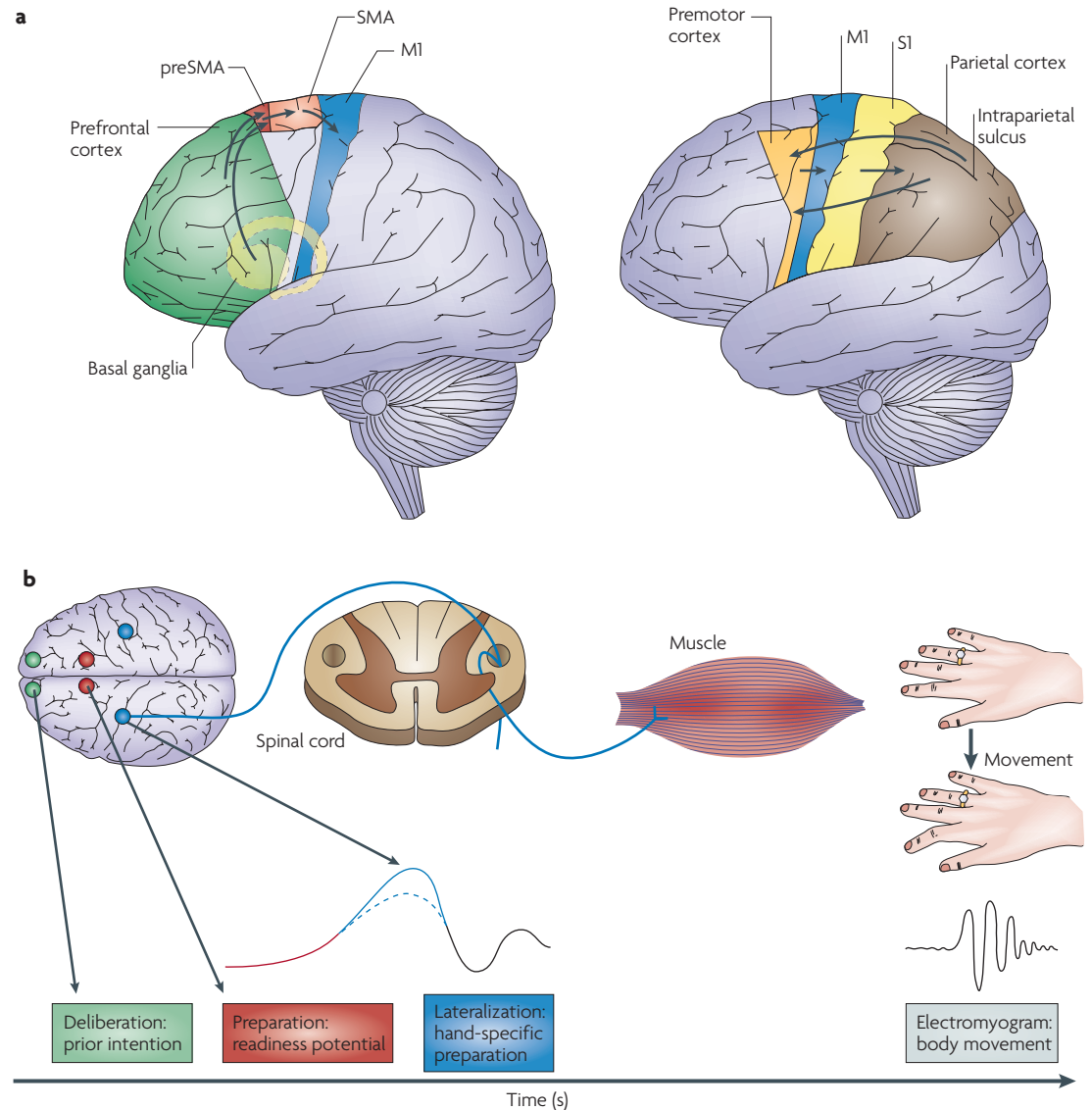


Figure 1 | Brain circuits for voluntary action. a | The primary motor cortex (M1) receives two broad classes of inputs. One key input (left-hand panel) reaches M1 from the supplementary motor area (SMA) and the pre-supplementary motor area (preSMA), which in turn receives inputs from the basal ganglia and the prefrontal cortex. In a second cortical network (right-hand panel), information from early sensory cortices (S1) is relayed to intermediate-level representations in the parietal cortex, and from there to the lateral part of the premotor cortex, which projects in turn to M1. This parietal–premotor circuit guides object-oriented actions, such as grasping, using current sensory input, but also contributes to some aspects of ‘voluntary’ behaviour. **b** | Brain activity preceding a voluntary action of the right hand. The frontopolar cortex (shown in green) forms and deliberates long-range plans and intentions. The pre-supplementary motor area (shown in red) begins the preparation of the action; together with other premotor areas, it generates the readiness potentials (red trace) that can be recorded from the scalp. Immediately before the action takes place, M1 (shown in blue) becomes active. In later stages of preparation the contralateral hemisphere is more active than the ipsilateral hemisphere; this is reflected in a lateralized difference between the readiness potentials that are recorded over the two hemispheres of the brain (solid and dotted blue traces). Finally, neural signals leave M1 for the spinal cord and the contralateral hand muscles. The contraction of the muscles is measured as an electrical signal, the electromyogram.

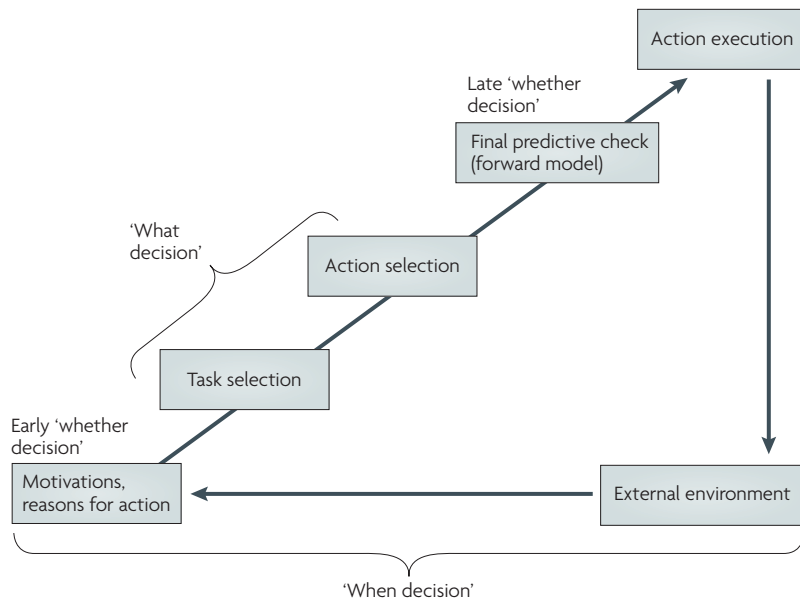


Figure 2 | A naturalized model of human volition. Volition is modelled as a set of decision processes that each specify details of an action. The decision whether to perform an action ('whether-decision') has both an early and a motivational component and a final predictive check. 'What decisions' specify which goal or task (from a range of tasks) to perform ('task selection') and the means by which to perform it ('action selection'). The timing of voluntary actions often depends on the combination of environmental circumstances and internal motivations: an explicit 'when decision' is not always necessary.

only to process information that is already present in the stimulus³³. The various action decisions that lead up to the performance of a voluntary action are described in the next sections.

Early 'whether decisions'. If an individual's current needs are satisfied, and if current stimuli are appropriately processed and responded to by routine schemas³⁴, then the individual's behaviour can be explained without recourse to any concept of volition. In other cases behaviour clearly goes beyond routine processing, such as when a new action is initiated or when an existing action pattern is withheld or modified. The brain then generates information according to a hierarchical set of decisions regarding the action, as schematized in FIG. 2. First there is an early decision whether to make any action at all. Needs, desires and other reasons for action have a strong role in this early decision. Voluntary actions might occur for any of three distinct reasons. First, routine processing of stimuli can fail to generate sufficient information to determine a response — for example, when selecting between two alternative actions in response to an ambiguous stimulus^{35,36}. Second, a new reason for action can suddenly emerge, reflecting either a renewed basic need, such as hunger, or a new high-level desire, such as the desire to wave to a friend. Third, a general drive to perform occasional voluntary actions would allow exploration of the behavioural landscape^{37,38}. In one important model of cognitive control³⁴, voluntary actions that occur for any of these reasons will temporarily suspend routine stimulus-based control and switch the control of the motor

apparatus from sensory to volitional input. A behavioural corollary of this switch may be the finding that reaction times for making a simple manual movement in response to a stimulus are higher when the stimulus occurs during preparation to make the movement voluntarily than when there is no preparation for the voluntary action³⁹.

'What decisions': goal selection. A further key decision relates to what voluntary action to perform. In fact, this decision has two forms: selecting between goals (or tasks) and selecting between movements to achieve them³⁶ (FIG. 2). Although people commonly maintain several goals simultaneously, voluntary actions are generally performed in series, so people must schedule goals by selecting between them. This aspect of action control has been largely ignored in the experimental literature, in which instructions usually specify a unique task. Neuropsychological studies, however, describe a dysexecutive syndrome, in which the order, scheduling and interaction of several tasks become disorganized⁴⁰.

Deciding between motor tasks seems to involve the frontal cortex. Evidence for this comes from two neuropsychological conditions that are seen in people with frontal lobe damage, particularly damage that involves the preSMA. Patients who exhibit utilization behaviour compulsively grasp and use objects in their immediate environment. Clinical reports suggest that they select as their task goal whatever is most salient in their current environment⁴¹, even when the object is not specifically drawn to their attention^{42,43}. In patients with anarchic hand syndrome, a unilateral frontal lesion leads to the contralateral hand automatically reacting to current stimuli, even when the patient explicitly states that they will not perform the action in question⁴⁴. Importantly, experimental studies of reaching show that even when these patients are instructed to perform a specific motor task, movements of their affected hand are captured by competing tasks, such as reaching for distractors^{45,46}. Moreover, action decisions made by patients with lesions in this area show unusual sensitivity to visual primes that were masked so as to be imperceptible. In healthy control participants, flashing a brief masked prime before a reaction-time task increased reaction times when the mask was compatible with the instructed stimulus, owing to automatic inhibition of motor programmes that are evoked by non-predictive and irrelevant primes⁴⁷. By contrast, in a patient with a preSMA lesion, masked primes speeded a subsequent motor response⁴⁸. This suggests that a normal function of the preSMA is to suppress automatic responding to current environmental stimulation, and that patients with preSMA damage are therefore hyper-responsive. These elegant experimental studies have the advantage that their results cannot be explained in terms of the unusual demand characteristics of the task or the patients not understanding what they are supposed to do: the patients did not consciously perceive the masked primes that influenced their behaviour.

Taken together, such findings suggest that the frontal lobes in general, and the preSMA in particular, have a crucial role in keeping volition focused and 'on

task', or in "binding intention and action" (REFS 49,50). Neuroimaging studies have shown that distinct caudal and rostral subregions of the preSMA are respectively active in voluntary selection between alternative tasks and in switching between such selections⁵¹. The ready distractibility of children with attention-deficit hyperactivity disorder may reflect a developmental disorder of the same system⁵².

'What decisions': movement selection. A second form of 'what decision' involves choosing between alternative means to achieve an identified goal; such movement decisions are clearly hierarchically secondary to decisions about goals (FIG. 2). Most goals can be achieved in any of several ways, in part because of the redundancy that is built into the motor apparatus. In computational models of motor control, an inverse model generates specific motor commands from a general goal description, such as 'reach for the object'. In the brain, this form of 'what decision' is thought to involve parietal and premotor areas in the dorsal visuomotor stream. Single neurons in the primate parietal cortex specify how a given target is achieved: Cui and Andersen³⁵ allowed monkeys to decide autonomously whether to indicate a target location by reaching to it or by making a saccade. They found that neurons in previously identified reach and saccade areas in the parietal cortex showed activity before a 'go' signal that predicted whether the animal would subsequently reach or saccade on a particular trial.

Many studies in both humans and animals have studied free choice between spatially defined responses, such as left and right key presses and leftward and rightward saccades^{6,31,51,53}. The neural codes that are associated with spatially distinctive actions are clearly identifiable: for example, parietal neurons have sensory receptive fields in contralateral space, and cortical motor areas project preferentially to the contralateral hand. However, the cognitive level of these decisions is unclear: sometimes left and right targets or responses constitute different tasks, whereas in other situations they are simply different means of performing a single task. Perhaps for this reason, the neural activity that is associated with spatially specific decisions seems to be widespread in the brain. In the frontal motor circuitry, left-right decisions have been associated with activity in the frontopolar cortex^{23,53}, the preSMA⁵³ and the rostral cingulate cortex⁵⁴; they have also been associated with lateralized readiness potentials recorded over M1 (REF. 6). Similarly, the parietal-premotor circuits that are associated with goal selection are also associated with spatially specific decisions^{55,56}. Although left-right decisions offer a convenient method for experiments, they can be difficult to locate in functional models of the information processing that underlies volition.

Recent computational models have considered how 'what task' and 'what movement' circuits might be linked. For example, Cisek has suggested that prefrontal-cortex signals bias the activation strength of a specific movement alternative that is coded in parietal-premotor circuits⁵⁷. A computational model of frontal-lobe function has suggested that the frontopolar cortex implements

goal selection by branching control towards the most rewarding of two task sets while keeping an alternative task set pending. In this model, the lateral prefrontal cortex guides actual behaviour according to the current task or goal⁵⁸. Although branching control towards the most rewarding of two current actions may not capture all of human voluntary action, the development of explicit computational models is a key step in developing scientific theories of volition.

'Late whether decisions': a final predictive check and veto. 'What decisions' generate information that activates specific motor outputs. However, the details of these outputs may not be predictable at the time that the initial decision whether to act is taken. Moreover, several brain networks independently generate different kinds of action information, so full descriptions of an impending action can be synthesized only very late. The cost of the selected action might turn out to be high, it might be a poor means to achieve the selected goal, or the task or environment might have changed. Therefore, once detailed information about voluntary action has been fully specified, a final check might occur before the motor system is committed and the gates to action execution are opened. In computational models of visually guided reaching, this check is achieved by comparing the output of a predictive forward model with a goal description; the motor commands are then adjusted according to the mismatch between the two⁵⁹. However, the same predictive checking process could be used not only to correct actions, but also to cancel ('veto') them completely. This second form of 'whether decision', which could be called a 'late whether decision' (FIG. 2), determines whether or not the action goes ahead. Most people recognize the situation of being about to say angry words or send an angry e-mail and refraining at the last moment (usually wisely!). Human studies of cancelling action have generally focused on responses to external 'no-go' or stop signals⁶⁰ and include studies of externally triggered stopping of internally generated actions⁶¹.

Libet reported a readiness potential that was consistent with motor preparation even on occasions in which a participant decided to veto the prepared action and did not actually move⁸. More recently, however, the neural substrate for the endogenous cancellation process itself has been identified. Brass and Haggard⁷ asked participants in a functional MRI (fMRI) experiment to prepare and perform simple key presses at a time of their own choosing, but to withhold the action at the last possible moment on some trials. Participants reported the time at which they felt they were about to move even on trials in which the movement was subsequently cancelled; this yielded an identifiable event for analysing brain activity in veto trials, which lacked any overt movement. An area of the anterior frontomedian cortex, rostral to the pre-SMA, was activated in veto trials more than in trials on which participants made an action (FIG. 3). This activation represents the neural correlate of a 'late whether decision'. Such decisions might have a key role in self control, and also raise the important possibility

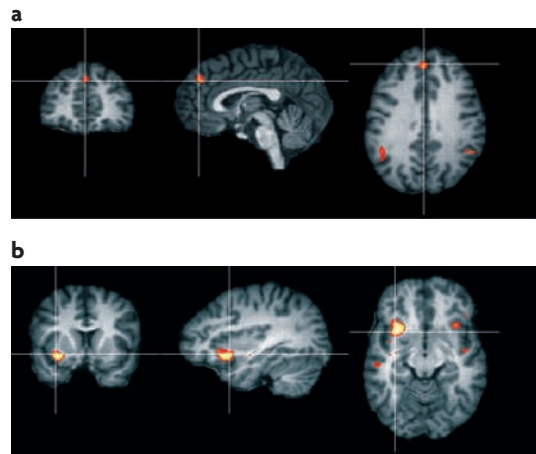


Figure 3 | Two brain areas activated by intentional inhibition of voluntary actions (veto). **a** | Activation in the frontomedian cortex for the contrast of veto versus action trials. **b** | Activation in the left and right anterior ventral insula for the contrast of veto versus action trials. Figure reproduced, with permission, from REF. 7 © (2007) Society for Neuroscience.

that voluntary actions can be prepared in order to simulate them but not execute them, as in imagined action or in prediction by forward models⁵⁹. In addition, veto trials showed a strong activation of the anterior insula⁷, consistent with an affective response to intentions that failed to drive actions.

‘When decisions’. Decisions about when to perform voluntary actions (FIG. 2) have attracted considerable attention and are an important experimental tool. Self-paced actions can be considered to be products of a ‘when decision’. Several studies have compared brain activity between self-paced conditions, in which the participant themselves decides when to make an action, and externally triggered conditions, in which the participant makes a similar action in response to a stimulus. Activity in both the preSMA¹⁷ and the dorsolateral prefrontal cortex²⁵ has been identified by this comparison. Studies that focused on voluntary action alone confirmed that the timing of an action can be predicted from preparatory activity in the preSMA^{23,62}. However, ‘when decisions’ in everyday life have a different form from ‘what decisions’ and ‘whether decisions’. Outside the laboratory, the timing of voluntary action generally depends on coordinating the scheduling of other potential actions and routine processes. ‘Whether decisions’ and ‘what decisions’ are made continuously in an iterative loop. The timing of a specific voluntary action often depends on external circumstances and internal motivations rather than on any explicit ‘when decision’. Therefore, an apparent ‘when decision’ to perform an action ‘now’ can sometimes be better described as a change in the evaluation of a ‘whether decision’ or a ‘what decision’. For example, deciding to quit in a gambling task might not involve an explicit ‘when decision’. Rather, the cost of action might escalate to the point that a ‘whether decision’ suggests inhibiting future action. Indeed, recent fMRI studies

show that decisions to quit and intentional inhibition have a common neural substrate in the frontomedian cortex^{7,63}.

One exception to this rule could be time-based prospective memory⁶⁴, which involves an explicit ‘when decision’ to perform an action at a specified later time. The anterior medial prefrontal cortex might hold intentions during a delay period between the initial decision regarding what to do and the later moment at which the action is executed⁶⁵. Interestingly, prospective-memory situations particularly highlight the need for ‘late whether decisions’ or ‘veto decisions’: an intention that is being maintained for later action might be dropped following re-evaluation.

General computational principles

FIGURE 2 identified the different types of decision that lead to voluntary action, but not the general computational principles by which these decisions are made.

Voluntary action as exploratory behaviour. First, innovative action has a clear survival advantage. An animal’s success depends on the balance between exploiting known resources through routine behaviour and exploring possible new resources through new actions³⁷. The generative, stimulus-independent quality of voluntary action resembles exploration rather than exploitation. Recent neuroimaging evidence confirms a dissociation in the frontal lobes between ventromedial frontal areas that code expected rewards and bilateral frontopolar regions that code exploratory choices³⁸.

Voluntary action as random behavioural noise. Second, intrinsic neural noise ensures an element of randomness in actions, which could explain why one action is chosen over another. Several experimental and computational studies suggest that there is competition between codes for alternative possible actions, such as movements to targets or to distractors^{66,67}. Inhibitory links between action codes mean that small, random variations in the activation level of one code can overcome the activation of another code by a ‘winner takes all effect’, which produces one result rather than another. For example, Cisek found that random variations in the firing of populations of neurons in the premotor cortex before a ‘go’ signal could predict which of two possible responses an animal would make⁶⁸.

Voluntary action as conditioned responding. Third, memory has a key role in determining action choices: in uncertain or ambiguous situations we generally do what was successful before in similar situations, or even repeat errors that we made previously. However, memories for previous stimuli and the reward values of their associated actions effectively reduce voluntary actions to stimulus-driven actions, in which the animal responds to an internal trace of the stimulus after some delay. Perhaps for this reason, autobiographical memory does not figure in cognitive theories of volition, although it plays a major part in psychological accounts of individual behaviour, notably in clinical psychology.

Voluntary action as goal-directedness. Finally, several accounts of voluntary action propose a teleological pull. These theories typically stress a strong linkage between cognitive representations of the goal of an action and the internal motor signals that cause the action. For example, ideomotor theories in cognitive psychology^{69,70} suggest that actions are represented in terms of their goals in the external world. However, teleological theories are at risk of dualistic thinking: if thinking about pressing a button really triggers a button-press movement of my finger, then there should be some account of the mechanism by which conscious states cause brain activity.

On the other hand, teleological theories fit well with associative accounts of operant action. An animal exploring its environment readily learns that an arbitrary action can produce rewarding outcomes⁷¹. Moreover, a conditioned stimulus elicits the same behaviours as an unconditioned stimulus: a pigeon will peck at the response key as if it were food, rather than just a means of acquiring food⁷². This process of ‘autoshaping’ suggests that a representation of the goal is indeed activated anticipatorily during action.

Teleological pull also appears in recent computational models that couple motor prediction to motor planning⁷³. Typically, action control begins with a sensory description of a ‘goal state’. Multiple inverse models generate motor command candidates that aim to achieve that state. The commands are passed from each inverse model to a

paired forward model that predicts their consequences. The actual motor command is a weighted sum of the output of all the inverse models. Models with predictions that are closer to the desired state receive higher weightings, and weightings can be biased by external contextual information. So, for example, if a to-be-grasped object is recognized as a cactus, the inverse model for ‘delicate precision grip’ is given higher weight than if it is not so recognized. This comes interestingly close to the role of memory in voluntary action (described above).

Such models are teleological in two ways. They initiate action by evoking an external goal, and they select between action candidates by evoking their external effects. Direct neural tests of teleological models can be difficult. However, they do make a key prediction about the brain, namely that the areas and circuits for planning voluntary movement should overlap with those for imagery and counterfactual thinking about the external world. Although fMRI studies confirm that frontal motor areas such as the preSMA are involved both in action planning and motor imagery⁷⁴, thinking about external events and effects may involve affective rather than sensorimotor regions of the prefrontal cortex⁷⁵.

Volition and consciousness

Voluntary actions are accompanied by specific subjective experiences. Indeed, the relation between these experiences and the brain activity that occurs before and during actions has been a key focus in the neuroscience of volition. The phenomenal experience of our own action is often not strong: psychologists often comment that motor control is ‘automatic’ and unconscious. Nevertheless, the experience of making a voluntary action is clearly different from that of an equivalent passive movement that is applied to the body: as Wittgenstein asked, “What is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?” (REF. 76). More importantly, the conscious intention to make an action seems to cause the action itself: we feel we have ‘free will’. Most neuroscientists are suspicious of this idea, because it implies a “ghost in the machine” (REF. 2). Rather, both conscious intention and physical movement might be consequences of brain activity. Wegner⁷⁷, for example, has proposed that the human mind assumes a causal path from conscious intention to action in order to explain the correlation between them. In fact, the correlation occurs because both conscious intention and action are driven by a common cause, namely the neural preparation for action. A more radical view⁷⁸ suggests that conscious intention is not a bona fide mental state at all, but rather an inference that is retrospectively inserted into the stream of consciousness as the hypothetical cause of the physical movement of our bodies. This view receives support from studies of psychosis, in which experiences of intention are associated with unusual causal explanations of connections between events^{79,80}. Even in the healthy brain, the consequences of an action can strongly influence the experience of the action itself^{81,82}. This influence is particularly strong in cases of action errors, in which feedback carries information about unexpected consequences of action⁸³ (FIG. 4).

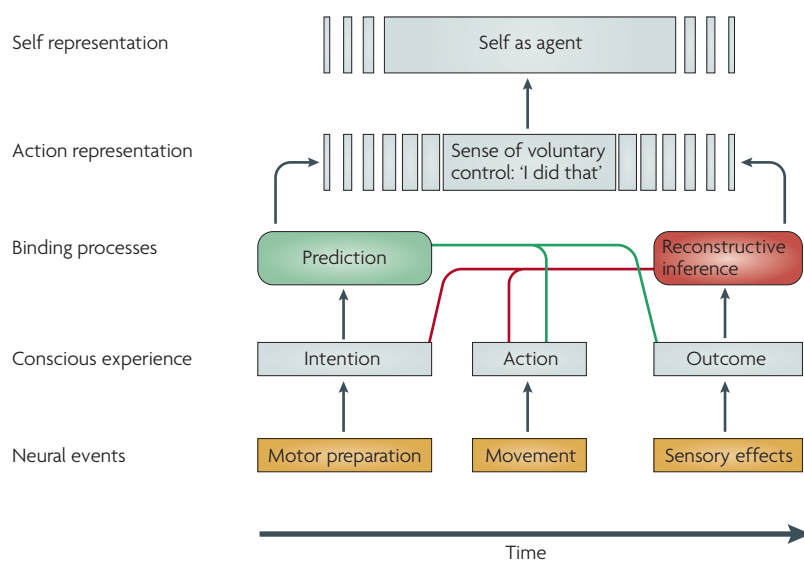


Figure 4 | Cognitive processes that underlie the experience of voluntary action. Neural signals that contribute to the experience of voluntary action include advanced preparation of action, reafferent somatosensory feedback, and sensory information about the effects of actions (bottom level). The separate experiences caused by these signals (second level) are synthesized to produce an overall impression of an action as a single event. Two specific cognitive processes contribute to this synthesis (third level). First, intentions predict the actions and the goal effects to which they refer (green lines). Second, the sensory experiences of the action and of its effects trigger a reconstruction of the intention to act (red lines). These processes bind together the various components of experience to produce an awareness of the action as a whole, compressed in time relative to the underlying neural processes (fourth level). This in turn produces a representation of the self as an agent that is capable of fluent voluntary control (top level).

In addition to the experience of intention, voluntary actions often produce an experience of agency. This is the experience that one's voluntary action causes specific events in the outside world. Agency necessarily involves the experience of external sensory consequences, whereas intention relates more closely to preparation and effort. The neural basis of agency remains unclear. Explicit attributions of sensory effects to one's own action or to another agent involve the parietal cortex^{84,85}, but the normal, implicit sense of one's own agency might involve predictions derived from intentions that are generated in the frontal motor areas⁸⁶. Here I focus primarily on the experience of intention rather than agency.

Features of conscious intention. In fact, voluntary action is linked to two quite different forms of conscious experience: long-range thoughts about future actions, and immediate feelings of being about to do something. Long-range intentions resemble plans and conscious deliberations and are linked to prospective memory. They also lack specific motoric information; rather, they involve mental time travel and a scheduling process that is similar to task selection. Current scientific research in long-range intentions focuses on identifying the brain mechanisms of prospective memory⁸⁷, and also involves comparative studies that investigate whether non-human animals show forethought^{88,89}.

Short-range intentions are closer to the present topic of voluntary action. These are often described in the literature as 'urges', although 'conscious intention' seems a more appropriate term. The experience of conscious intention has attracted considerable scientific interest, but clear descriptions of the phenomenology have been attempted only recently⁹⁰. There are at least three aspects to the phenomenal content of conscious intention: timing, effector specificity and intensity. Conscious intentions seem to occur during a brief window approximately 1 s before movement onset⁴. They include specific details about the body part involved and the movement that will occur⁹¹. Finally, conscious intentions clearly come by degrees: one can be barely conscious that one is going to take the next step when walking, but intensely aware of pulling a trigger. The intensity dimension of conscious intention has hardly been studied experimentally. However, clinical studies of patients with tic disorders describe premonitory urges, the intensities of which increase before the tic behaviour begins. Interestingly, these urges are body-part specific and can even have a sensory character⁹².

The timing of conscious intention has been studied to clarify the causal relations between conscious thought, brain activity and voluntary movement. In Libet's well-known experiment⁴ (BOX 1), participants make voluntary hand movements at a time of their own choosing and later report the reading that a clock showed when they first experienced the 'urge to move'. Although the experiment raises several methodological concerns (BOX 2), the results suggest that conscious intention is experienced a few hundred milliseconds before the action occurs. Because the brain preparation for such actions, as measured by readiness potentials, frequently begins 1 s

or more before the action occurs, the conscious intention cannot be the cause of the neural preparation or of the action. The experiment is sometimes considered a neuroscientific disproof of the concept of 'free will', although the conceptual details of this argument are hotly disputed⁷⁸.

Could the conscious intention to move be part of a psychological narrative, which participants create to explain why their hand suddenly moved? Certainly, events that occur after action contribute to the experience of intention¹⁰⁴. However, best evidence against retrospective interpretations comes from studies in which the motor areas of the brain are artificially stimulated as part of neurosurgical treatments. For example, when Fried and colleagues stimulated the preSMA, patients reported 'an urge' to move a specific part of the contralateral body⁹¹. As they had not yet actually moved, this could not be a retrospective intervention. When more-intense stimulation was applied through the same electrodes, the corresponding part of the patient's body indeed moved on five of the six stimulations that were reported as producing both urge and movement. It is unclear whether the urge reported by the patients resembled the normal conscious experience of intending to act. Moreover, the experience evoked by stimulation might arise not in the preSMA itself, but in remote areas connected to it, such as the parietal cortex⁹³. However, such studies do at least suggest that a conscious experience akin to intention is part of the normal neural preparation for voluntary movement.

Libet *et al.*'s approach has also been extended to investigate the content and neural basis of intention. Haggard and Eimer⁶ asked participants to choose voluntarily between left and right key-press actions in a modified version of Libet's task. They showed that judgements of conscious intentions correlated not with the onset of the midline readiness potential, but with the onset of the 'lateralized readiness potential' (the later phase of preparation, in which brain activity contralateral to the selected hand exceeds ipsilateral activity). This result confirmed that an experience of conscious intention is tied to the specific body movement that is prepared, rather than to a general preparation to move.

Soon *et al.*²³ recently reported a 'mind-reading' version of the same experiment that used fMRI. They identified patterns of brain activation before movement that best predicted whether participants would perform a forthcoming action with the left or right hand. In addition to the activations of preSMA and contralateral motor cortices (which were predicted by readiness-potential findings), they found patterns of activation in the frontopolar cortex that predicted participants' choices 8 s before the action itself was performed. These patterns may represent an earlier stage in the causal chain that generates actions (see above). Neural processes such as the readiness potential must clearly have antecedent causes, and more-sensitive measurement techniques may reveal the earlier stages in the chain. Alternatively, these very early activations might be associated with forethought and longer-range conscious intention, as the same brain areas are known to be involved in prospective memory⁸⁷. Although the

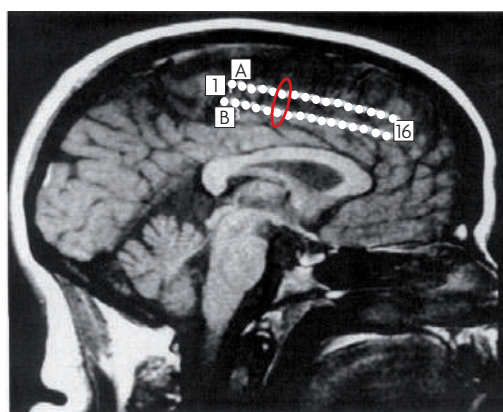
instructions in such experiments typically tell participants to decide spontaneously (if instructed spontaneity is possible!), prior deliberation cannot easily be excluded.

Libet himself suggested that the interval between conscious intention and movement onset was sufficient to allow a process of conscious veto, which would inhibit an impending action before execution⁸. Such 'free won't' would have the philosophical advantage of salvaging traditional concepts of moral responsibility. However, dualism about conscious veto is just as problematic as dualism about conscious initiation of action. It is unclear how a

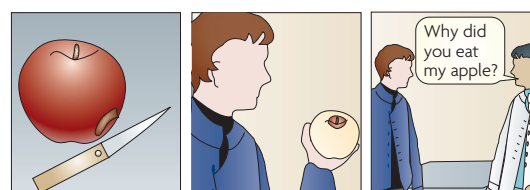
conscious veto might influence brain activity. Moreover, the veto, like the conscious intention, could itself be a consequence of some preceding unconscious neural activity⁹⁴. The processes of voluntary inhibition of voluntary action are demonstrated in recent neuroscientific studies of the prefrontal cortex^{7,95}. These processes might provide the final check, or 'late whether decision', before voluntary action (see above). They might be associated with specific conscious experiences, both of the impending action and of the decision to abandon it. But they do not imply any unusual or dualistic form of mind–brain causation.

Box 2 | The preSMA: a key structure for voluntary action

a Conscious intention



b Action inhibition

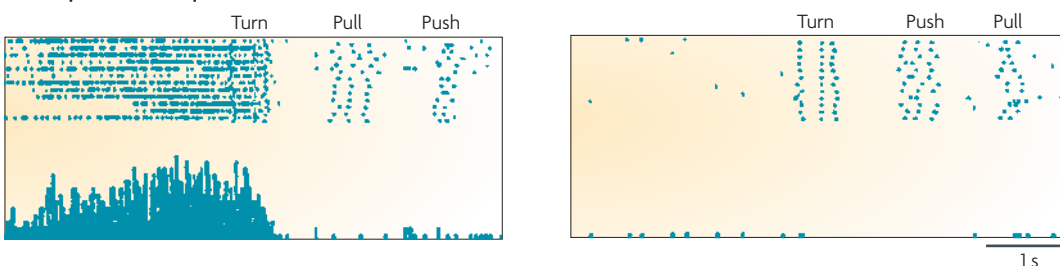


While being tested, patient CU spotted an apple and a knife left on purpose on a corner of the testing desk.

He peeled the apple and ate it. The examiner asked why he was eating the apple.

He replied: "Well ... it was there." "Are you hungry?" "No, well a bit." "Have you not just finished eating?" "Yes." "Is this apple yours?" "No." "And whose apple is it?" "Yours, I think." "So why are you eating it?" "Because it is here."

c Complex action sequences



The pre-supplementary motor area (preSMA) is located between the 'cognitive' areas of the frontal lobes and motor-execution areas, such as the SMA proper and the primary motor cortex⁹⁹. It occupies a key position in the frontal network that transforms thoughts into actions (see figure). Direct stimulation of the preSMA through electrodes (red circle in part **a** of the figure) produces both a feeling of a conscious 'urge to move' and, at higher current, movement of the corresponding limb^{91,100}. However, many neurological studies suggest that the main function of the preSMA is to inhibit actions rather than cause them. Lesions in this area can produce automatic execution of actions in response to environmental triggers. For example, when the patient sees a cup, they will reach for it and attempt to drink even if they do not wish to (for another example, see figure, part **b**)^{44,49}.

Studies in animals and humans suggest two further roles for the preSMA, which seem to be quite different from its role in voluntary action. Single neurons in the monkey preSMA code for the preparation of entire complex sequences of movements (see figure, part **c**, which shows preSMA activation during a turn movement that is followed by a 'pull' movement but not when the turn movement is followed by a 'push' movement), and also code for transitions between movements within the sequences¹⁰¹. Transcranial magnetic stimulation studies in humans also indicated a role for the preSMA in the preparation of entire sequences, but not in transitions within sequences¹⁰². The brain areas that allow voluntary control of action also seem to combine individual actions into more complex ones. Volition may have arisen as a result of this capacity for increasingly complex action. This suggestion receives support from the classic finding that monkeys with lesions of Brodmann's area 6, including the preSMA, are unable to flexibly adjust the pattern of their movements when they fail to achieve a goal¹⁰³. Instead, the monkeys repeatedly make the same stereotyped and unsuccessful action. Thus, voluntary action is largely a matter of finding convenient ways to get actions to fulfil current goals. Part **a** of the figure reproduced, with permission, from REF. 91 © (1991) Society for Neuroscience. Text in part **b** of the figure from REF. 43. Part **c** of the figure reproduced, with permission, from REF. 101 © (1994) Macmillan Publishers Ltd.

Box 3 | Responsibility for action

All known human cultures have the concept that an individual is responsible to society for their actions. This in turn rests on a concept of volition: individuals control their own actions, and their conscious knowledge of what they are doing should allow them to choose between right and wrong actions. Thus, in systems based on Roman Law, committing a crime generally requires both a physical action (*actus reus*) and the conscious experience of performing the action (*mens rea*). Views on the psychology of intention and action are thus engrained in the language that is used to discuss morality and responsibility.

However, the links between conscious intention, physical action and responsibility are both problematic and highly important. Intention without action is sometimes sufficient for responsibility and sometimes not. For example, it is widely held that thought alone is not a crime. Someone who wants to hit another person but holds back at the last moment has not acted and therefore cannot be responsible. In other situations, preparation that is relevant to an action can be thought sufficient for responsibility, even if the planned action is prevented. Recent terrorism trials provide a topical example. Equally, action without intention is sometimes judged sufficient for responsibility and sometimes not. A person may be judged not guilty of an action that they clearly committed if they were not consciously aware of their actions, such as in sleepwalking assault. Although neuroscientific descriptions of the brain circuits that generate action and conscious awareness can contribute an evidence-based theory of responsibility, it is unclear whether they can capture all the nuances of our social and legal concepts of responsibility.

This Review has resisted the traditional, philosophical idea that conscious thoughts cause voluntary actions, in favour of a neuroscientific model of decisions about action in relatively unconstrained situations. How might this model relate to responsibility? The initial 'whether decision', based on reasons and motivations for action, and the final check before action are both highly relevant to responsibility. By contrast, decisions regarding how and when an action is performed are less crucial. Responsibility might depend on the reason that triggered a neural process culminating in action, and on whether a final check should have stopped the action. Interestingly, both decisions have a strong normative element: although a person's brain decides the actions that they carry out, culture and education teach people what are acceptable reasons for action, what are not, and when a final predictive check should recommend withholding action. Culture and education therefore represent powerful learning signals for the brain's cognitive-motor circuits. A neuroscientific approach to responsibility may depend not only on the neural processes that underlie volition, but also on the brain systems that give an individual the general cognitive capacity to understand how society constrains volition, and how to adapt appropriately to those constraints. A basic level of functioning of the social brain, as well as the cognitive-motor brain, is essential for our conventional concept of responsibility for action.

Conclusions and future directions

Voluntary action is one of the most characteristic features of the human brain. Modern neuroscience rejects the traditional dualist view of volition as a causal chain from the conscious mind or 'soul' to the brain and body. Rather, volition involves brain networks making a series of complex, open decisions between alternative actions. The preSMA is a key node in the network of areas that contribute to these decisions. Future investigations should focus on decisions to inhibit voluntary action, and the contribution of predictive monitoring; these decisions involve a medial prefrontal area, anterior to the classical preSMA.

One reason for the neurosciences' lasting fascination with volition is the central role of conscious experience in voluntary action. This is now being studied systematically as an important brain datum, whereas in the heyday of behaviourism it was dismissed as a mere illusion. Future

neuroscientific work could benefit from the development of rigorous approaches to the phenomenology of action, including better measurements of conscious experience.

Neuroscientists study systems by the classic engineering principle of intervening to control inputs and then measuring outputs. Only a few special situations, such as neurosurgical exploration and brain-computer interfacing, allow interventive control of the human voluntary motor system. Well-designed scientific studies that use these situations could provide new insights into the volitional brain.

Finally, modern neuroscience is shifting towards a view of voluntary action being based on specific brain processes, rather than being a transcendental feature of human nature. This will have important ethical implications for the interactions between brain science and wider society, and will inform discussion at the societal level about individual responsibility (BOX 3).

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