Sense of agency in the human brain

Patrick Haggard

Abstract | In adult life, people normally know what they are doing. This experience of controlling one's own actions and, through them, the course of events in the outside world is called 'sense of agency'. It forms a central feature of human experience; however, the brain mechanisms that produce the sense of agency have only recently begun to be investigated systematically. This recent progress has been driven by the development of better measures of the experience of agency, improved design of cognitive and behavioural experiments, and a growing understanding of the brain circuits that generate this distinctive but elusive experience. The sense of agency is a mental and neural state of cardinal importance in human civilization, because it is frequently altered in psychopathology and because it underpins the concept of responsibility in human societies.

The sense of agency is the feeling of making something happen. It is the experience of controlling one's own motor acts and, through them, the course of external events. The term 'sense of agency' has also been used with a rather different meaning in both social science[1] and computational[2] literatures, in which it typically designates a felt capacity to act (self-efficacy), without reference to any specific motor act. Here, however, I focus on the experience that occurs before, during and after actual muscular movement, rather than on beliefs or facts about potential actions. Thus, I use the term sense of agency to refer to an experience that accompanies the performance of a specific motor act.

Many voluntary actions are 'phenomenally thin' (REF. 3), because the experiences that accompany them are not particularly vivid. However, the conjunction of several different aspects of this experience is normally jointly sufficient to produce a feeling of control over what one is doing, even if one is doing it 'automatically' (REF. 4). The neural computations that produce this experience are so efficient and so familiar that our sense of agency can seem to be minimal and banal. However, a simple example demonstrates the importance and careful construction of the sense of agency. When it gets dark, I may reach out to switch on the light, perhaps barely aware that I am acting at all. However, if my hand fails to touch the switch, or if the light fails to come on (or if someone else switches the light on just before I do using another switch), I will experience a striking conflict and violation of expectations as a result of the mismatch between the intended and actual result of the action. In this scenario, the normal experience of fluently controlling the environment is suddenly interrupted as the sense of agency is lost.

The sense of agency underpins many important features of human societies. In law, for example, criminal responsibility requires not only that an agent performs a specific motor action but also that they 'know the nature and quality of the act'. This implies that the agent should experience a sense of agency with respect to their action[5,6]. Many technologies, from simple tools to social media interfaces, can extend the sense of agency from the experience of controlling the immediate environment through one's own movements to controlling much wider environments, or even virtual environments. In a major epidemiological study of work and well-being, a strong sense of agency (gained, for example, by making one's own decisions rather than executing routine tasks) was identified as a major determinant of health[7]. Disruptions of the sense of agency (for example, in movement disorders or as a result of psychopathology) have major implications for quality of life[8].

Perhaps because of its pervasive and foundational quality, sense of agency has received surprisingly little attention in cognitive neuroscience research until recent times. However, in the past two decades, neuroscientists have made greater efforts to understand the brain processes that produce sense of agency. In this Review, I describe how the sense of agency can be operationally defined and measured in experimental laboratory settings. I consider the different signals and cognitive processes that generate a sense of agency over one's own actions and outcomes, along with the specific brain areas and circuits that implement these computations. Disruption of these circuits may explain the altered sense of agency that frequently accompanies psychopathology. I end by discussing the importance of sense of agency in normative concepts at the level of entire societies, such as legal responsibility.

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Instrumental control
The capacity to initiate an action and thus bring about an intended change in the environment.

Volition
The process of preparing, initiating and executing an action under one's own control. Traditionally, the hallmark of volitional action is that the agent 'could have done otherwise', implying that the action was not directly caused by the current stimulus environment.

Mirror self-recognition
The capacity to recognize a visual percept as being related to one's own body. This has traditionally been assessed by a test in which a coloured mark is placed on a body location, such as the forehead, and subsequently viewed via a mirror. Only if the animal recognizes the body in the mirror as its own, will it try to remove the mark.

Most previous psychological and neuroscientific studies have used explicit judgements attributing actions to particular agents to study sense of agency[9,10]. However, in this Review, I focus primarily on the experience of instrumental control over an external object or event, rather than on the attribution of authorship and on implicit measures of sense of agency.

Defining the sense of agency

Most, but not all, actions are accompanied by characteristic subjective experiences that vary in their content and their salience. These may include the experiences of intending to act, of choosing to make one particular action rather than another and of initiating or triggering the action. These types of experience are essentially cognitive and have been linked to action preparation in the frontal lobes and to a motor command from the primary motor cortex[11,12]. They can be classed as 'central' experiences. In addition, the sense of agency typically also involves a further class of experience that is associated with the body actually moving and is relayed by the activity of peripheral somatosensory receptors. Interestingly, involuntary movements (such as reflexes and movements evoked by brain stimulation) typically produce these 'peripheral' experiences but not central experiences. Such involuntary movements are never accompanied by a sense of agency, although they are generally accompanied by what philosophers have called a sense of 'ownership' (REF. 13). Ownership refers to the feeling of 'mineness' — that is, the feeling that an object (for example, a body part or a mental state) is specifically linked to one's self[13].

The sense of agency thus seems to involve both ownership, with respect to an experience of body movement ('my body moved'), and the cognitive experience of voluntary control over that body movement ('I voluntarily made it move'). The latter element has been described as the experience of oneself being the 'source of the action' (REF. 14). This definition suggests a sense of ownership of the voluntary motor command itself, recalling both classical notions of will and neurophysiological descriptions of internally generated action[15]. As I describe below, recent neuroscientific evidence confirms the key role of brain circuits for voluntary action in producing a sense of agency.

The core of sense of agency, therefore, is the association between a voluntary action and an outcome. Interestingly, the importance of volition in agency is also recognized by the 'voluntary act condition' in criminal law. According to this, individuals can only be responsible for their own voluntary actions and not for their reflexes, sneezes or similar movements[16] (BOX 1). Wittgenstein famously asked "What is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?" (REF. 17). One possible answer might be: a sense of agency. Psychologists have noted that the sense of agency is strongest when there is a strong motivation to act, a clear action goal and a specific cortical motor command that initiates the action[18]. However, the precise definition of a voluntary action remains controversial. Some neuroscientists suggest that a voluntary action is one that requires neural activity in cognitive motor areas[19]. Others have eschewed the concept of voluntariness altogether and have instead defined a class of endogenous, or 'internally generated', actions that contrast with reactions to an external stimulus[11]. Philosophers have used quite different criteria: for example, some insist that voluntary actions can only be defined on the basis of the subjective knowledge of the agent[20]. A full discussion of the neuroscience of volition can be found elsewhere[11,21,22].

A final and important aspect of sense of agency is the experience of how one's action affects the external environment. Through their actions, humans and other animals can transform the world around them and also experience how they have transformed it.

Measuring the sense of agency

Any scientific account of sense of agency requires some way to measure it. The simplest measure of an individual's sense of agency is the answer to the explicit question "Did you do that?" Making such a judgement requires one to attribute sensory events to one's own intentional action rather than to some other cause (FIG. 1). This process thus resembles mirror self-recognition[23,24]. Many experimental studies that have used explicit measurements of sense of agency are fundamentally social, in the sense that agency is attributed either to oneself or

Box 1 | Agency and voluntary control in law courts

All legal systems have some concept of criminal responsibility. This concept asserts that healthy adults have a conscious experience and knowledge of their own intentions, actions and outcomes that underpin their voluntary control of the action. Systems of law descending from Roman law use the term *mens rea* to describe this subjective, intentional aspect of responsibility. In principle, therefore, someone who lacks a sense of agency regarding an action cannot be held criminally responsible for that action. In practice, courts are rightly sceptical when defendants claim that they did not experience what they were doing: there is an obvious secondary gain that is associated with such a claim, and lack of volition and agency are difficult to prove objectively. The legal concept of *mens rea* also contrasts with neuroscientific views that emphasize the automatic, unconscious precursors of actions that are experienced as voluntary[43,95,96].

However, the law acknowledges some situations in which voluntary control and agency over action are reduced. Such cases can often be understood in terms of interactions between limbic and motor systems in the brain. Past homicide cases have considered whether factors such as age (and thus the maturational state of the brain) or circumstances that induce intense emotion or involve prolonged abuse can alter these limbic–motor interactions and thus influence voluntary control of action[97–99]. For example, prolonged abuse can induce profound changes in cognitive and behavioural capacity, similar to the 'learned helplessness' condition that is described in animal behaviour research[100]. Thus, homicide in such cases could be viewed as analogous to a 'fight' response to threat, which may replace the more normal 'flight' response under conditions of extreme stress.

In English law, the defence of 'provocation' was recently replaced by a 'loss of control' defence[101]. It was recognized that actions following prolonged abuse (and not only actions made in the sudden heat of the moment) may not meet normal conditions of voluntary control and responsibility. Interestingly, rats with previous experience of control over a stressor acquired resilience against effects of subsequent uncontrollable stress[102]. Past history of agency may thus be strongly neuroprotective in situations of uncontrolled stress. Conversely, sustained abuse might remove the resilience that, under normal circumstances, allows a degree of self-control even in occasional situations of high stress, threat or emotion. This could provide a neural basis for considering duration of abuse as a relevant 'qualifying trigger' for actions involving loss of control. However, this area of law remains highly controversial, and the relevance of neuroscientific evidence is, correctly, a topic of intense debate.

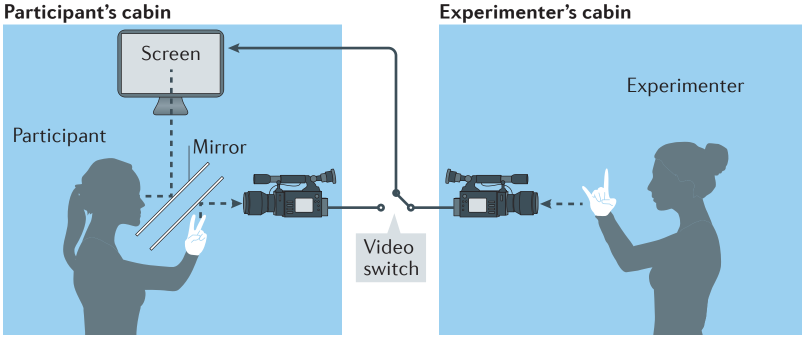

Figure 1 | **Explicit judgments of agency.** Action-recognition experiments can be used to examine explicit judgments of agency. In a typical example of this type of experiment, participants are asked to judge whether a video that they are watching shows their own hand movements or those of another person. Participants are asked to make a specific pattern of hand movement. A screen is connected to a video switch (controlled by the experimenter), allowing the participant to see either their own hand or the hand of an experimenter wearing an identical glove. The experimenter performs either the same hand movement as the subject or a different hand movement. If the participant reports that they are viewing their own hand action, they attribute authorship of the viewed action to themselves. Adapted from Sirigu, A., Daprati, E., Pradat-Diehl, P., Franck, N. & Jeannerod, M., Perception of self-generated movement following left parietal lesion, *Brain*, 1999, **122** (Pt 10), 1867–1874, by permission of Oxford University Press.

to another person. As noted by Marc Jeannerod, in this type of task, the brain networks for sense of agency function as a 'who' system[25].

Studies using explicit agency judgements show a consistent cognitive bias: there is a tendency to overestimate one's own agency and to misattribute to oneself events that are unrelated to one's own action[26,27]. Strikingly, this bias is stronger when the outcome of an action is positive, rather than neutral or negative, suggesting a powerful 'self-serving' mechanism through which positive affect influences sense of agency[1]. Explicit judgements of agency in social situations may be particularly distorted by such secondary gain. For example, political leaders consistently attribute economic upturns to their own political actions[28].

Given these limitations, it has been proposed that the sense of agency should instead be investigated by implicit measures. Although explicit judgements of agency are rare in everyday life, we experience a clear feeling (or 'buzz') of agency during everyday actions, even when no evaluation or judgement is required[29]. Implicit measures aim to capture this feeling without requiring people to explicitly think about agency or control. They thus potentially avoid some of the cognitive biases and desirability effects that affect explicit judgements. Interestingly, implicit and explicit measures tend to be only weakly correlated across individuals[30], although both seem to be sensitive to factors such as reward (including self-serving bias, as described above)[31,32], action–outcome interval[33] and the actual degree of instrumental control[33].

One putative implicit marker of agency focuses on distortions of time perception. Programming actions[34], executing actions[35] and predicting their outcomes[36] all influence time perception. In experiments focusing on the 'intentional binding' effect, participants are asked to report the perceived time either of a voluntary action or of a subsequent sensory event (such as a tone). It has been shown that voluntary actions, but not involuntary movements, are perceived as shifted in time towards their subsequent outcomes and that the outcomes themselves are perceived as shifted towards the voluntary actions that caused them, in comparison to control conditions in which the action and outcome occur independently[37] (FIG. 2a). As a result, the sense of agency can be quantified as a compression of the perceived interval between action and outcome[38] (FIG. 2b). Many factors influence time perception, including attention, causality, pharmacological agents and adaptation. Therefore, shifts in time perception are not diagnostic of a sense of agency. However, a difference in intentional binding between two appropriately chosen conditions can potentially be interpreted as a difference in sense of agency.

The experience of instrumental control that is typically investigated in experiments such as intentional binding is largely independent of the process of social attribution to agents and explicit judgement. To take an example from daily life, someone cycling up a hill may experience a strong sense of agency that is based on perceiving how their actions affect the speed of the bike. This process does not invoke any other agent, any social aspect or any explicit propositional judgement.

The two different approaches to the measurement of agency allow us to investigate an important distinction in the psychology of action between one's own instrumental agency (self to world control) and social attribution (self or other). This distinction has long been recognized in philosophy and psychology[39], but it remains unclear whether social attribution of actions to agents depends on an antecedent ability to compute and perceive instrumental agency, or vice versa. This Review focuses on the sense of agency that is associated with instrumental control, as distinct from the notion of agency based on social attribution.

Cognitive processes that drive agency

Volition and action preparation. As noted above, a genuine sense of agency clearly requires some internal state of volition, conation or 'urge'. Involuntary movements, such as those caused by brain stimulation or passive displacement of a body part, do not produce a sense of agency. For example, studies of the intentional binding effect show that involuntary movements produce less binding than do voluntary actions, or even reverse the effect entirely[31,40].

Recognizing the distinctive neural events that accompany volitional, as opposed to involuntary, movements is therefore important for our understanding of sense of agency and may also be an important element in learning voluntary control of movement[41] (BOX 2). Preparatory activity in cognitive motor areas has been considered characteristic of voluntary action. For example, the readiness potential, a characteristic slow negative electroencephalographic potential that occurs before movement, has classically been taken as a marker of volition[42] (for a contrary view, see REF. 43). In one recent study, participants who showed a strong early rise in the readiness potential also showed stronger intentional binding between actions

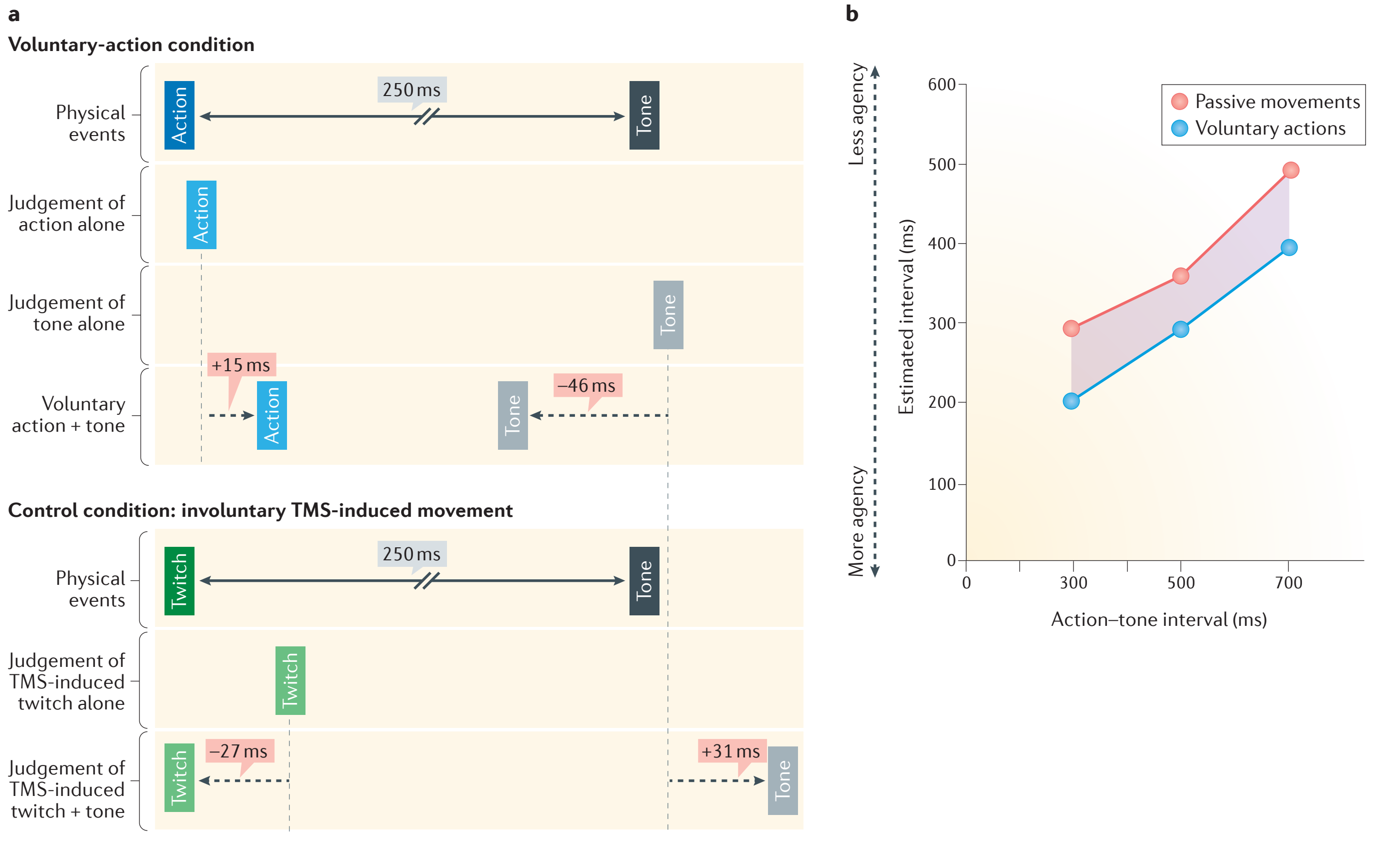

Figure 2 | **Measuring sense of agency implicitly. a** | The schematic shows how the intentional binding task can provide an implicit measurement of sense of agency[45]. In this task, participants view a small rotating clock hand. They make a self-paced button-press action, which triggers a tone 250 ms later (physical events indicated by the dark blue and grey boxes). Thus, participants are expected to experience a sense of agency over the tone. They report the time at which they pressed the button or at which they heard the tone, in separate blocks of trials. First, the participants are asked to estimate the clock time at which they made the action or heard the tone in separate baseline conditions in which only the action or only the tone occurs (estimates indicated by the light blue and grey boxes). Next, in the experimental conditions, the participants themselves cause the tone by their own action and judge either the time of the action or the time of the tone. In this case, the perceived times of the action and tone shift closer to each other (indicated by the dashed arrows, not drawn to scale), relative to the baseline conditions. This produces an intentional binding effect. Replacing the intentional action with a physically similar but involuntary movement (a twitch evoked by transcranial magnetic stimulation (TMS) of the motor cortex) has the opposite effect (dark and light green boxes indicate the time of the actual twitch versus the estimated times of the twitch). Thus, sense of agency can be measured implicitly and quantitatively using the magnitude of perceptual shifts in action and tone timing. **b** | In an interval-estimation paradigm, participants give an absolute verbal estimate of the delay (in ms) between a key-press action and a tone that follows after a short but somewhat variable delay. Lower estimated delays correspond to a greater sense of agency[93]. Thus, estimates are shorter for a voluntary key press than they are in a control condition in which the finger is passively pushed onto the response key. The actual intervals between key press and tone are randomized but are always shorter than 1 second to prevent counting. Part **b** is adapted with permission from REF. 38, Elsevier.

and outcomes, implying an increased sense of agency[44]. According to this view, the cognitive preparation that precedes voluntary action may also contribute to sense of agency over an outcome. However, mere temporal coincidence between an involuntary movement that is evoked by transcranial magnetic stimulation (TMS) and ongoing preparation of voluntary action was not sufficient to produce intentional binding[45]. The cognitive preparation of an action plan needs to match the muscular movement precisely to elicit an experience of agency.

Transcranial magnetic stimulation
(TMS). A technique in which a strong magnetic field is applied to the scalp to influence neural activity in a cortical area beneath. If ongoing cognitive performance is impaired, the affected cortical area is assumed to be necessary for the task.

Action selection: choosing what to do. Choosing between alternative possible actions strongly influences sense of agency[46]. Importantly, this influence must be prospective, because the processes that select between alternative actions necessarily precede movement and outcome. During action selection, the dorsolateral prefrontal cortex (DLPFC) is thought to assemble a 'response space', a set of alternative possibilities from which the desired action must be chosen[47]. Some studies suggest that the DLPFC not only represents possible alternative actions but also houses the process of selecting between them[48]. However, medial frontal areas have also been argued to contribute to the action-selection process[49,50].

Several lines of evidence suggest that the processes of selecting between alternative actions in the frontal lobe strongly contribute to sense of agency. A recent paper[51] meta-analysed seven studies that combined anodal transcranial direct current stimulation (TDCS) over the left DLPFC with intentional binding measures. TDCS enhanced intentional binding only in those studies in which participants themselves selected between alternative actions.

Box 2 | Acquiring a sense of agency

A newborn infant seems to have little or no voluntary control over its actions and little or no sense of agency. Classical theories of psychological development suggest that voluntary control of actions (notably, smiling) emerges in the first months of life and is guided by the reinforcement of parental affective communication[103,104]. This observation suggests that humans learn to become agents over their own bodies and thus over their external environment (including their caregivers). This initial learning generally predates first autobiographical memories; however, the learning process continues well into adulthood. Indeed, some legal systems acknowledge fully developed sense of agency and responsibility only after 18 years of life[105]. The case of Christy Brown, who was born with cerebral palsy and was only able to move his left foot, offers an interesting insight into the transformative power of sense of agency. In his autobiography, Brown recalls the moment of his first instrumental action — using his left foot to seize a piece of chalk from his sister's hand and draw a squiggle. He describes this first experience of agency as the starting point of a virtuous cascade of escalating achievements that was recognized and encouraged by others, and that culminated in a successful artistic career[106].

The same progressive trajectory of agency occurs in individual learning and on an evolutionary scale. For example, tool use can be seen as an evolutionary adaptation that extended the range of an animal's agency[107,108]. Humans, and perhaps some other primates, can learn and exploit arbitrary associations between actions and outcomes. As a result, they retain a clear sense of agency, even when using sophisticated technologies to act at a distance[109]. The recent development of brain–machine interfaces offers novel examples of learning a sense of agency. Paralyzed individuals can learn to control a neuroprosthesis by thought[110]. Anecdotal evidence suggests that these patients report a feeling of agency for actions using the prosthesis. Although no human studies have yet systematically explored how this experience emerges during learning, rodent models suggest that the plasticity of corticostriatal connections has a key role in acquiring neuroprosthetic agency[111]. Once the basic cognitive capacity of instrumental control develops, it seems to transfer successfully to novel brain codes for action, as well as to arbitrary outcome events. The dramatic pace of human technological achievement suggests that the cognitive mechanisms underlying instrumental agency may be almost unlimited in scope.

Transcranial direct current stimulation
(TDCS). A non-invasive brain stimulation technique in which a small current passes between electrodes that are positioned on the scalp. Anodal stimulation is thought to increase excitability of the underlying cortex, whereas cathodal stimulation may reduce excitability.

Efference copy
A copy of the outgoing (efferent) motor command from the brain to the muscles. An efference copy, in conjunction with a forward model, can be used to predict the sensory consequences of action.

Prediction error
The difference between the actual outcome of an action and the predicted outcome. Neural signalling of prediction error can be used to adjust and improve performance, and also to learn how to improve future predictions.

Action-selection processes could affect sense of agency in several ways. When alternative actions consistently cause specific corresponding outcomes, then the ability to select which action to make gives the agent some actual statistical control over the outcome, thus increasing the sense of agency by increasing the likelihood that the outcome will match that desired. For example, in one study, a specific electroencephalographic component (the auditory N1) that was evoked by a tone was more strongly attenuated when the tone reliably corresponded to whichever of four actions that participants had selected compared with when it did not[52]. Such sensory attenuation is thought to occur when a prediction of the outcome of one's action makes reafferent perception of the actual outcome redundant. The exact relation between sensory attenuation and sense of instrumental agency remains unclear (see below), but this finding demonstrates the important relation between action selection and action–outcome prediction.

Action-selection processing might also directly influence sense of agency, irrespective of the relation between the selected action and its outcome. According to this view, fluent action selection (which corresponds to certainty about which action to make) boosts the feeling of control over the outcome of the action that is made. Several recent studies used subliminal visual priming to demonstrate that the sense of agency depends on metacognitive signals that are generated during action selection. For example, briefly presenting and then masking a right-pointing arrow can reduce manual reaction time to a subsequent, supraliminal right-pointing 'target' arrow and increase reaction time to a left-pointing target arrow. Unseen primes can also bias 'free' choices between left-hand and right-hand responses[53]. Interestingly, the same primes can influence explicit judgements about the sense of agency[54]. Congruent priming boosted explicit judgements of agency over a visual event that occurred as an outcome of the manual response, relative to incongruent priming. Crucially, the primes did not directly predict the identity of the visual outcome, and further experiments ruled out the possibility that participants simply monitored their reaction times and used motor performance as a proxy for agency[55]. Thus, action-selection processes seemed to generate an internal, metacognitive signal indicating the level of fluency or conflict that is involved in selecting an action from the response space. These action-selection signals contributed to judgements of agency, even though the difficulty of action selection was entirely independent of the actual statistical relation between action and outcome. The contribution of action-selection fluency to sense of agency is, in a sense, illusory. Just knowing what action to make does not guarantee the action outcome. However, as with many illusions, it may be a rule of thumb that normally works for typical agency situations.

The comparator model of agency

As described above, a sense of agency is generated when voluntary actions match outcomes. In computational models of motor control (FIG. 3), motor commands are used to predict the sensory consequences of action[56]. This prediction is thought to involve passing an efference copy of the motor command to a 'forward model' (also known as an 'internal predictive model') of the moving body part[57]. Sensory information about the body and the environment is then compared with the sensory feedback that would be predicted given the motor command. The result of this comparison is known as a prediction error. For example, when the brain sends the motor command to reach for the light switch, one might predict the resulting movement of the arm and also that the lights will come on. If the arm does not move in the appropriate way, the motor control system must update or alter the motor command to achieve the goal of switching the lights on.

Comparator models were originally developed to explain how the brain monitors and corrects goal-directed movements. However, the same models have also been used to explain the sense of agency. If an event is caused by one's own action (and if the internal predictive model is correct), the actual feedback corresponds exactly to the prediction, and the result of the comparison is zero; otherwise, the result is a non-zero prediction error.

According to this view, people have a sense of agency over events that can be predicted given their motor commands. In one series of studies, the comparator model was used to explain how people attribute visual feedback to their own action or to the action of another

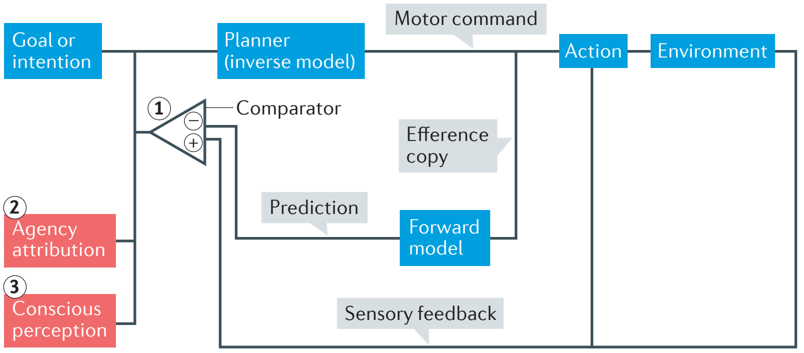

Figure 3 | **The comparator model for neural control of action and agency.** In the comparator model of action control, an action begins with an intention or desired goal state. An inverse model computes the motor command that is required to achieve the goal state (or at least to approach it) and generates the motor command that will drive the action. A forward model uses a copy of the current motor command (known as an efference copy) to predict the probable sensory consequences of the command[56]. This prediction is compared with sensory feedback signals that provide information about the ongoing action and about its effects on the external environment. The result of the comparison can be used in three ways: to adjust the current motor command (**1**); to attribute agency for actions and environmental events (**2**) (if the comparator gives a result of zero then the event is caused by one's own action); and to attenuate predictable, self-produced sensations (**3**).

agent (FIG. 1). The comparator model suggests that people compare the visual feedback predicted from their own motor commands with the movement that they see[9,58]. Any mismatch in this comparison justifies the attribution "that is not me" implying a reduced or absent sense of agency[24]. Temporal cues can have a particularly important role in action attribution[59]. The time of initiating an action allows a precise prediction about the time of the outcome[60,61]; thus, any temporal mismatch in the visual feedback of actions reduces the sense of agency.

Interestingly, according to the comparator model, the sense of agency is caused by the lack of any prediction error, implying absence of any signal at the output of the neural comparator. These models may therefore successfully explain the phenomena of 'non-agency', such as the striking feeling that "I did not do that, something is going wrong!", when actions fail and generate a prediction-error signal. However, they may be less convincing as explanations of the 'buzz' of agency in routine, successful action[29], as the model does not generate any neural signal that could cause this experience. Furthermore, comparator models attenuate, or even entirely suppress, perception of action outcomes: according to these models, we only perceive what we cannot predict, as the content of perception is given by the difference between actual and predicted feedback. This suppression can be functional: for example, it prevents perceptual overload during self-generated action[61]. However, it seems to be counterintuitive to attenuate the perception of the very goal events that are the targets of volition. If the sense of agency depended only on comparator mechanisms, the experience of the fruits of one's own agency would be tantalizingly suppressed. Indeed, taking this interpretation to an extreme, human endeavour might disappear if agents never became aware of the success of their actions.

For these reasons, it has been suggested that the comparator model may apply primarily to the immediate sensorimotor effects of movement[56,62] and may attenuate only high-intensity action outcomes[63]. By contrast, people can experience a sense of agency over arbitrary outcomes long after the action occurred. This suggests that cancellation of reafference against predictions cannot be the only process contributing to sense of agency.

Prospective versus retrospective agency

The different signals within the sensorimotor system that are thought to underpin the sense of agency become available at different times: premotor signals (such as those associated with action selection by the inverse model) occur before action, whereas sensory feedback signals occur after the action and its outcome. Feedback signals are further affected by any delay in the causal chain between action and outcome, and by delays in receiving and processing reafferent sensory information. Comparator models deal with this temporal misalignment by delaying the output of the forward model until it can be compared to delayed outcome feedback[64]. Therefore, the sense of agency can be computed only after delayed outcome feedback has reached the comparator. This implies that people experience a sense of agency only retrospectively, after the event[65]. This view receives support from the fact that explicit judgements of agency attribution are readily biased. For example, priming participants with the effect of a subsequent action increases their sense of agency over the action[66], even when the primes are below the threshold for conscious perception[67]. Strong advocates of this view claim that actions are triggered by environmental influences and premotor processes that operate largely outside of consciousness. Thus, the brain generates a sense of agency through retrospective inferences about one's own action authorship after the fact, but it does not have access to any direct readout or signal about the true origins of actions, or does not use these signals when computing sense of agency[65].

Some recent studies suggest that the sense of agency also depends on prospective signals (FIG. 4). Most experimental measures of sense of agency are unable to separate the effects of prospective and retrospective components of agency. However, studies of intentional binding have distinguished between these two components by varying the probability that a voluntary action produces a tone. For example, one study showed that, when the probability that a tone would follow an action is 50%, the binding of the action towards the tone is stronger in trials on which tones are actually presented than in trials without tones[68]. This suggests that the tone retrospectively altered the perceived timing of the action that caused it. Similar effects, in other studies, have been described as 'postdiction' (REF. 69). Interestingly, the action binding on those trials in which no tone in fact occurred depended on the probability of tone occurrence: binding was stronger on blocks in which the probability of a tone following an action was high (75%) rather than low (50%)[68]. This finding suggests that an additional, prospective component of the sense of agency is present even if the outcome does not in fact occur. This experiment provided strong evidence that the experience of one's own actions is fundamentally linked to the prediction of the outcomes of those actions and not just to retrospectively inferring agency once outcomes are known.

Brain mechanisms underlying agency

Neuroimaging studies have played an important part in identifying the brain areas that implement the various cognitive and computational processes underlying sense of agency. These studies have consistently highlighted the role of the parietal cortex in sense of agency. Early studies that used explicit agency-attribution judgements identified strong activation of the angular gyrus in the inferior parietal lobe in situations in which visual feedback was judged as unrelated to one's own action[58,70]. A recent meta-analysis of 15 neuroimaging studies confirmed the temporoparietal junction area, including the angular gyrus, as the neural correlate of 'non-agency' (REF. 10). Some of the studies included were based on experimental factors that are known to influence sense of agency, such as delayed sensory feedback, rather than on actual subjective reports about agency. The studies also generally focused on retrospective components of the sense of agency (that is, on judging whether a stimulus was self-generated or not). Interestingly, the temporoparietal junction also responds to unexpected external sensory events in the absence of voluntary action[71]. Therefore, its activation in situations of non-agency may not reflect the process of attributing agency but rather one possible result of that process (namely, the judgement that an event is externally caused). Interestingly, medial and lateral prefrontal areas were also associated with non-agency over outcomes in some of the studies[10]. The only area that was consistently associated with positive self-agency was the anterior insula, possibly reflecting a general role of this area in ongoing self-awareness[72].

A recent event-related functional MRI experiment suggested that the angular gyrus may also contribute to the prospective sense of agency. In this study[73], researchers used subliminal priming to alter the fluency of action selection. Participants made left-hand and right-hand key presses in response to arrow stimuli. Their actions lead, after a delay, to one of a number of colours appearing on the screen. An unseen, subliminal prime arrow presented just before the imperative stimulus could facilitate or hinder the participants in selecting and making the appropriate action, depending on whether the subliminal prime arrow was compatible or incompatible with the imperative stimulus. Compatible primes led to faster reactions than incompatible primes[74]. More interestingly, compatible subliminal primes also led to a stronger sense of control over the colour patch caused by the participant's action. Functional MRI analysis focused on the brain activations that are associated with action selection. The angular gyrus was more strongly activated when participants gave low agency ratings, rather than high agency ratings, but only when the subliminal prime was incompatible with the supraliminal imperative stimulus. Thus, the angular gyrus may monitor signals that are generated by conflict arising during action-selection processes in frontal areas. This hypothesis was supported by an increased functional connectivity between the angular gyrus and the lateral PFC during incompatible trials. Furthermore, TMS of the angular gyrus at the time of presentation of the primes abolished the tendency to give lower agency ratings on incompatible trials[75]. Thus, the parietal cortex may not simply match outcomes to actions retrospectively; it may also receive prospective signals about ongoing processing for the selection and initiation of action. Because this prospective component can be measured independently of actual contingencies between actions and outcomes, it could be considered metacognitive.

The contribution of frontal and prefrontal lobes to sense of agency remains less clear. These areas have a crucial role in planning and initiating a voluntary action[7]. Many experimental designs use manipulations that influence both the frontal processes that generate motor actions and those that generate the subjective experience of agency. These designs cannot distinguish between direct effects on sense of agency and indirect effects that are mediated by changes in action control. However, some recent studies combining non-invasive brain stimulation with implicit measures of sense of agency have focused specifically on the experience of agency. It was shown[76] that TDCS over the pre-supplementary motor area, a medial frontal area that is strongly implicated in both volition and sense of agency, reduced the intentional binding effect, and particularly the binding of actions towards outcomes. In another study, theta-burst TMS over the pre-supplementary motor area reduced the binding of outcomes towards actions[77]. Finally, as described above, a recent meta-analysis[51] suggested that action-selection processes in the DLPFC make a specific contribution to the sense of agency.

These recent studies thus provide an overall picture of the brain networks underlying sense of agency. Prospective signals alone can provide only estimates about instrumental control over external events: the chain of causation may go awry, or one may be unable to track the causal chain correctly[78]. Inferences based on retrospective signals alone seem to misclassify many events as self-caused when they are not. Therefore, a combination of prospective and retrospective signals seems to be necessary to reliably compute one's own agency. The parietal cortex plays a key part in monitoring multiple signals relevant to sense of agency, including signals of selection, volition and initiation that are generated in the frontal cortices[79]. According to one view[79], the parietal lobe acts as a comparator model, comparing intentional signals with sensory feedback signals. However, this account cannot explain why parietal activations strongly depend on the results of the comparison, rather than on the process of comparison itself. In particular, several studies showed stronger parietal involvement for a sense of non-agency than for positive sense of agency[9,58].

Comparator models of agency encourage the search for a single brain site where intention and feedback are matched. However, an alternative view treats agency

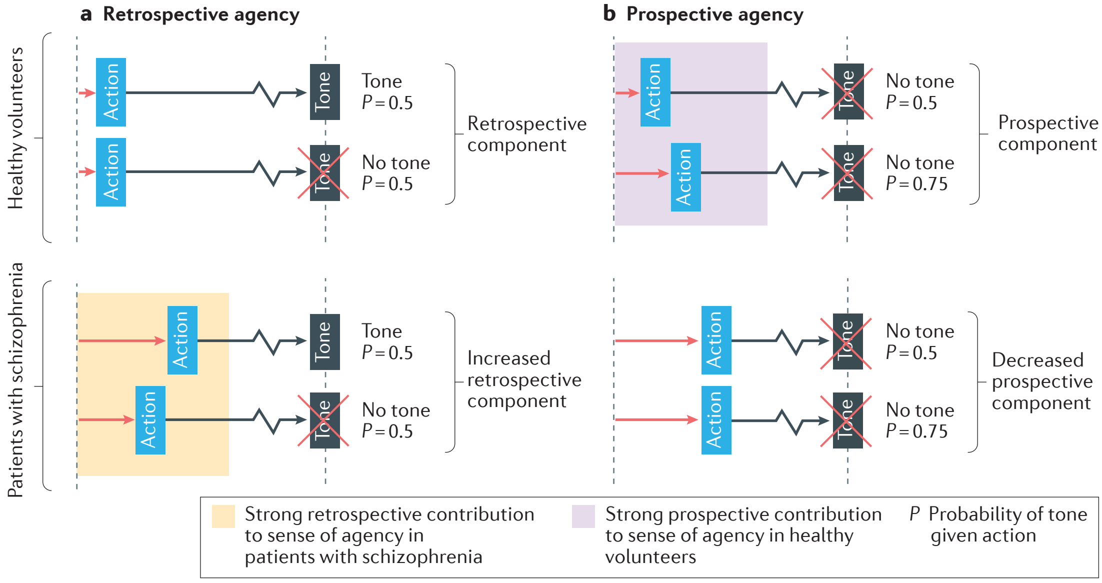

Figure 4 | **Prospective and retrospective agency.** The schematics illustrate the results of an experiment that used the intentional binding effect to distinguish between prospective and retrospective components of the sense of agency. **a** | Voluntary actions were followed by tones in 50% of trials (trials chosen at random). In healthy volunteers, the perceived time of the action (blue rectangles) was shifted towards the tone (red arrows, not drawn to scale) and independent of whether the tone occurred or not. In patients with schizophrenia, the perceived time of the action showed a general shift towards the time of the tone (grey rectangles), perhaps indicating poor attention to time. Crucially, the perceived time of action was shifted more in trials in which the tone actually occurred than in trials in which it was omitted. Thus, for the patients with schizophrenia, the tone triggered a retrospective reconstruction of the experience of the action. **b** | To assess prospective components of sense of agency, the perceived time of action was compared between two blocks of trials, which differed in the probability that the action would cause a tone. Only the trials in which no tone actually occurred are shown. In healthy volunteers, the perceived time of action showed stronger shifts when a tone was highly likely to occur than when the tone was less likely to occur. Thus, the strength of predictions about the tone influenced the experience of action. This prospective aspect of sense of agency was absent in patients with schizophrenia. These results suggested that the sense of agency in healthy volunteers is based on predictions that use knowledge about action–outcome relations, whereas the sense of agency in patients with schizophrenia is based on retrospective reconstruction. Adapted from Voss, M. *et al.*, Altered awareness of action in schizophrenia: a specific deficit in predicting action consequences, *Brain*, 2010, **133**, 3104–3112, by permission of Oxford University Press.

as a subjective consequence of an association between action and outcome rather than as a result of difference signals between predicted and actual outcome. Such associations might link the prospective premotor signals arising from action selection and initiation to the retrospective, perceptual signals arising from body movement and external outcomes. The key neural correlate of sense of agency might lie in the connectivity between frontal and prefrontal motor areas that initiate action and parietal areas that underlie the monitoring of perceptual events, rather than in any single structure. A recent study on sense of agency in psychosis (see below) strongly supports this connectivity view.

Pathological sense of agency

Several neurologic and psychiatric conditions involve pathology of sense of agency. Clinical neurology broadly classifies movement disorders as either hyperkinetic or hypokinetic. A similar classification can be made for the subjective experience of action. Some conditions are hyperagentic (involving an excessive experience of one's own causation and control over events), whereas others are hypoagentic (involving reduced experience of causation and control). One account of depression notes that depressed individuals experience less control over outcomes than do healthy individuals[80] but attributes this to a hyperagentic bias of healthy individuals. According to this view, which has remained controversial, depressed individuals have a realistic assessment of how limited their agentic capacity really is.

Most research on pathology of agency has focused on schizophrenia. The German psychiatric tradition uses the term *Ich-Störung* to refer to a range of disturbances of selfhood, self-world boundary and self-agency. For example, patients suffering from delusions of control may have the feeling that their thoughts and actions are not their own but are instead transmitted or caused by external agents. According to one model[81], such symptoms arise from a failure to predict the consequences of self-generated actions. In the absence of appropriate predictions, sensory experiences that are caused by one's own actions and thought processes are not cancelled by any internal prediction and are perceived as external events. Several lines of evidence have supported this view. Patients with schizophrenia have shown an impaired ability to detect when visual feedback of their movements

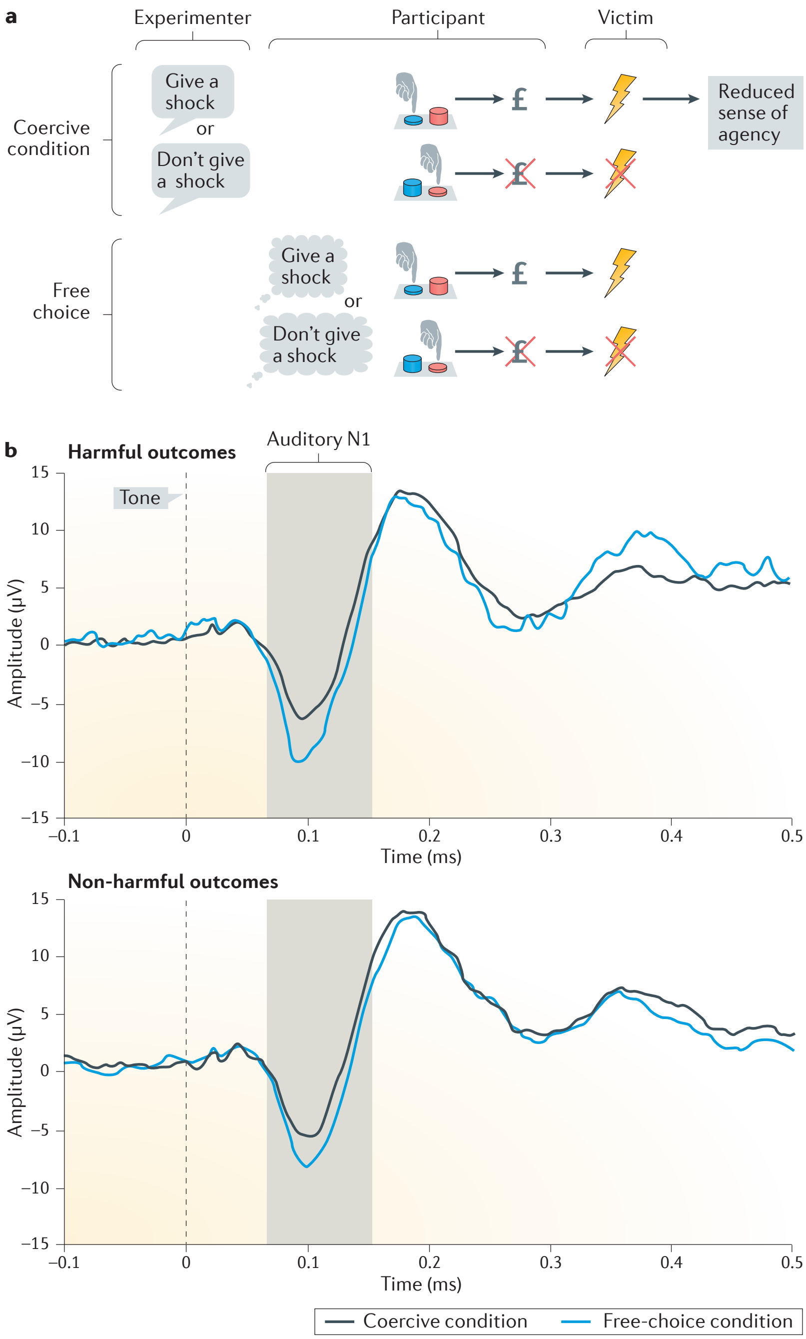

Figure 5 | **Coercion reduces sense of agency. a** | The schematic illustrates an experiment testing the effects of coercion on sense of agency[92]. The participant was asked to estimate the time interval between a button press and a tone. In the coercive condition, the experimenter told the agent which key they had to press before each trial. One key would deliver a painful electric shock to a 'victim' at the same time as the tone and also bring the agent a financial reward. Another key delivered no shock to the victim and earned the agent no money. In a free-choice condition, the agent could choose between the same two keys, and the experimenter gave no instructions. The agent's estimates of intervals between action and tone were significantly greater when they were coerced into giving the victim a shock than when they freely chose to do so, suggesting a reduced sense of agency under coercion. **b** | Event-related potentials (ERPs) evoked by the tone are shown. Coercive instructions reduced the amplitude of auditory N1 component of the ERP, suggesting that the neural processing of action outcomes was reduced in the coercive condition compared with a free-choice condition. This effect was seen both when the action lead to a painful shock and when it did not. Part **b** is reproduced with permission from REF. 92.

had been modified[82] or was not linked to their own action[83]. Intriguingly, they also lacked the sensory attenuation of self-generated action consequences, a key feature of the comparator model of predictive motor control[84–86].

These results would suggest a reduced sense of agency in psychosis. However, a recent study found that the intentional binding effect in a small sample of patients with positive symptoms was stronger, rather than weaker, than in healthy volunteers[87]. Underestimation of time intervals seems to be a general characteristic of some patients with schizophrenia[88]: indeed, the patients showed a stronger binding between two successive tones, in the absence of action, than did healthy individuals. However, the between-group difference in binding was greater for action–tone intervals than for tone–tone intervals. In a larger, more recent study, it was shown that the main distortion of sense of agency in schizophrenia may lie not in the strength of the agency experience but in the cognitive processes that produce it[89]. In an experiment designed to isolate the prospective and retrospective components of the sense of agency (see above and FIG. 4), the intentional binding of actions towards tones in patients with schizophrenia depended entirely on the actual occurrence of the tone. By contrast, in the healthy volunteers, action binding depended on the probability that the tone might occur and was largely independent of whether the tone actually occurred or not on any individual trial. That is, the patients' sense of agency was based largely on retrospective reconstructions of the experience of action, driven by occurrence of the outcome, whereas the healthy volunteers' sense of agency was based on predictions about probable outcomes. Psychosis thus seemed to abolish the normal prospective element of agency that characterizes healthy adult life. In this sense, the results of binding and sensory attenuation experiments agree: in schizophrenia, the brain may be in a constant state of surprise, attempting to understand the events that it has itself generated.

Society, agency and responsibility

Most human societies adhere to the concept of individual responsibility for action. This forms the basis for praise and blame, punishment and reward. Individual responsibility depends on the assumption that most, or all, individuals experience a sense of agency over their actions and outcomes. In fact, courtroom pleas of 'guilty' or 'not guilty' are explicit judgements of agency. Few mental states thus sustain such a strong social superstructure as the sense of agency. The 'voluntary act condition' in law[16] insists that an individual can only be criminally responsible for actions that they consciously decide to perform with a reasonable understanding of the probable outcome. The emerging field of 'neurolaw' has highlighted the relationship between legal concepts of responsibility and individuals' cognitive capacity to experience agency[90]. For example, the law acknowledges diminished responsibility for homicidal action on the grounds of 'loss of control' in a small number of specific cases, such as self-defence or persistent abuse (BOX 1). Does such 'loss of control' represent involuntary recruitment of a specific neurobiological system

Event-related potential
An electrical potential that is generated in the brain as a consequence of neuronal activity becoming synchronized by the external stimulus. Event-related potentials are recorded by averaging electro-encephalographic measurements recorded at the scalp and time-locked to a stimulus, and consist of precisely timed sequences of waves or 'components', which may each reflect a specific cognitive process in the brain.

Instrumental actions
Actions that produce a direct or indirect consequence on an animal's external environment. The transformation of the environment is the goal of the action.

subserving 'flight-or-fight' action control or merely a cultural expectation about when extreme behaviour might actually become acceptable? These explanations need not be exclusive: the law can be seen as a normative constraint on basic neurobiological drives to action.

In other controversial cases, defendants have denied responsibility by claiming that they were only obeying orders. This implies that the sense of agency for one's own actions may be reduced under conditions of coercion, which could in turn explain why people seem to comply rather readily with coercive instructions[91]. On the other hand, this defence could simply represent a disingenuous attempt to avoid blame by claiming a reduced experience of agency. Accordingly, an experimental design was recently developed in which an experimenter gave instructions to one participant to deliver visibly painful shocks to another participant[92] (FIG. 5). Because the participants took turns in the roles of giving and receiving shocks, each had direct experience of the unpleasant effects of their own actions on their co-participant. Participants estimated the brief delay that elapsed between their action and an auditory tone that occurred synchronously with the delivery of the shock. The subjective duration of this interval provides an implicit measure of sense of agency, analogous to intentional binding, with intervals initiated by voluntary actions being perceived as shorter than equivalent intervals initiated by passive movements[93,94] (FIG. 2b). Coercive instructions increased the perceived duration between action and tone–shock, relative to free choice, indicating that coercion reduced sense of agency. Strikingly, coercive instructions also resulted in lower event-related potential responses to the tone, suggesting a suppression of neural processing of action outcomes. This implies that obeying instructions reduces the sense of agency, producing an experience that is closer to passive movement than to voluntary action.

Previous research had shown that increasing the number of action alternatives from which a participant could freely select leads to an increase in sense of agency[46]. Reduced sense of agency under coercion is consistent with the possibility that social coercion effectively constrains an individual's free choice[47]. The finding does not, of course, legitimate the defence of 'only obeying orders', but it does explain how acting under coercion can lead individuals to experience a psychological distance from unpleasant consequences of their actions. It also demonstrates how social situations can strongly influence an individual's sense of agency, and thus their feelings of responsibility.

Conclusion

The human sense of agency is not a transcendental feature of human nature but the result of specific activity in the brain circuits that underlie voluntary motor control. Frontal and prefrontal areas select and initiate intentional actions, and convey information to parietal areas that monitor intentions, actions and outcomes. This circuit operates both prospectively (in advance of actions) and retrospectively (to monitor whether an action has achieved the intended outcome). The computational flexibility of this circuit probably underlies the human capacity to develop a sense of agency when using advanced technologies that involve arbitrary and indirect relations between actions and outcomes. Recent psychological research has emphasized that sense of agency can result from post hoc inference and is prone to illusions[65]. However, this argument has perhaps been overstated. In fact, the premotor signals related to selection and initiation of the motor command have an important role in sense of agency for the thousands of simple instrumental actions that adult humans execute each day. The distinctive experience of initiating a voluntary motor action seems to be necessary, although not sufficient, for sense of agency in normal circumstances.

Concepts of individual responsibility for action play a crucial part in the systems of law that underpin functional human societies. Individual responsibility relies heavily on brain mechanisms underlying sense of agency. Growing neuroscientific knowledge about the neural mechanisms of agency will lead to increasingly sophisticated manipulations of the subjective experience of agency, both technologically and socio-politically. Therefore, this area of neuroscience has profound ethical implications at the level of the individual, the society and indeed our species as a whole.

1. Bandura, A. Self-efficacy mechanism in human agency. *Am. Psychol.* **37**, 122–147 (1982).
2. Friston, K. *et al.* The anatomy of choice: active inference and agency. *Front. Hum. Neurosci.* **7**, 598 (2013).
3. Tsakiris, M. & Fotopoulou, A. in *Decomposing the Will* (eds Clark, A., Kiverstein, J. & Vierkant, T.)103–117 (Oxford Univ. Press, 2013).
4. Broadbent, D. E. Task combination and selective intake of information. *Acta Psychol. (Amst.)* **50**, 253–290 (1982).
5. Rex v. M'Naghten (*UKHL J16*) www.bailii.org http://www.bailii.org/uk/cases/UKHL/1843/J16.html (1843).
6. Garrison, A. H. The history of the M'Naghten insanity defense and the use of posttraumatic stress disorder as a basis of insanity. *Am. J. Forensic Psychol.* **16**, 39–88 (1998).
7. Marmot, M. G. *et al.* Health inequalities among British civil servants: the Whitehall II study. *Lancet* **337**, 1387–1393 (1991).
8. Frith, C. D., Blakemore, S. J. & Wolpert, D. M. Abnormalities in the awareness and control of action. *Phil. Trans. R. Soc. Lond. B* **355**, 1771–1788 (2000).
9. Farrer, C., Bouchereau, M., Jeannerod, M. & Franck, N. Effect of distorted visual feedback on the sense of agency. *Behav. Neurol.* **19**, 53–57 (2008).
10. Sperduti, M., Delaveau, P., Fossati, P. & Nadel, J. Different brain structures related to self- and external-agency attribution: a brief review and meta-analysis. *Brain Struct. Funct.* **216**, 151–157 (2011).
11. Passingham, R. E. & Wise, S. P. *The Neurobiology of the Prefrontal Cortex: Anatomy, Evolution, and the Origin of Insight* (Oxford Univ. Press, 2014).
12. Sherrington, C. S. *The Integrative Action of the Nervous System* (Yale Univ. Press, 1906).
13. Gallagher, S. Philosophical conceptions of the self: implications for cognitive science. *Trends Cogn. Sci.* **4**, 14–21 (2000).
14. Marcel, A. J. in *Agency and Self-Awareness: Issues in Philosophy and Psychology* (eds Roessler, J. & Eilan, N.) 48–93 (Oxford: Clarendon Press, 2003).
15. Passingham, R. E., Bengtsson, S. L. & Lau, H. C. Medial frontal cortex: from self-generated action to reflection on one's own performance. *Trends Cogn. Sci.* **14**, 16–21 (2010).
16. Hart, H. L. A. in *Punishment and Responsibility* 90–112 (Oxford Univ. Press, 1960).
17. Wittgenstein, L. *Philosophical Investigations* (Basil Blackwell, 1967).
18. Bandura, A. Social cognitive theory: an agentic perspective. *Annu. Rev. Psychol.* **52**, 1–26 (2001).
19. Fried, I., Mukamel, R. & Kreiman, G. Internally generated preactivation of single neurons in human medial frontal cortex predicts volition. *Neuron* **69**, 548–562 (2011).
The authors, following Libet's classical volition experiments, used intracranial recordings to show that the activity of a small number of medial frontal neurons suffice to predict the moment of conscious intention that precedes a voluntary action.
20. Ford, A. in *Essays on Anscombe's Intention* (eds Ford, A., Hornsby, J. & Stoutland, F.) (Harvard Univ. Press, 2011).
21. Haggard, P. Human volition: towards a neuroscience of will. *Nat. Rev. Neurosci.* **9**, 934–946 (2008).
22. Pacherie, E. The phenomenology of action: a conceptual framework. *Cognition* **107**, 179–217 (2008).
23. Gallup, G. G. J. Chimpanzees: self-recognition. *Science* **167**, 86–87 (1970).
24. Sirigu, A., Daprati, E., Pradat-Diehl, P., Franck, N. & Jeannerod, M. Perception of self-generated movement following left parietal lesion. *Brain* **122**, 1867–1874 (1999).
25. Georgieff, N. & Jeannerod, M. Beyond consciousness of external reality: a 'who' system for consciousness of action and self-consciousness. *Conscious. Cogn.* **7**, 465–477 (1998).

26. Tsakiris, M., Haggard, P., Franck, N., Mainy, N. & Sirigu, A. A specific role for efferent information in self-recognition. *Cognition* **96**, 215–231 (2005).
27. Wegner, D. M. & Wheatley, T. Apparent mental causation. Sources of the experience of will. *Am. Psychol.* **54**, 480–492 (1999).
This influential paper provided early experimental evidence favouring the view that the sense of agency is retrospectively inferred from outcomes rather than being directly perceived.
28. Horne, A. *Macmillan: The Official Biography* (Macmillan, 2008).
29. Synofzik, M., Vosgerau, G. & Newen, A. Beyond the comparator model: a multifactorial two-step account of agency. *Conscious. Cogn.* **17**, 219–239 (2008).
30. Dewey, J. A. & Knoblich, G. Do implicit and explicit measures of the sense of agency measure the same thing? *PLoS ONE* **9**, e110118 (2014).
31. Yoshie, M. & Haggard, P. Negative emotional outcomes attenuate sense of agency over voluntary actions. *Curr. Biol.* **23**, 2028–2032 (2013).
32. Takahata, K. *et al.* It's not my fault: postdictive modulation of intentional binding by monetary gains and losses. *PLoS ONE* **7**, e53421 (2012).
33. Berberian, B., Sarrazin, J.-C., Le Blaye, P. & Haggard, P. Automation technology and sense of control: a window on human agency. *PLoS ONE* **7**, e34075 (2012).
34. Hagura, N., Kanai, R., Orgs, G. & Haggard, P. Ready steady slow: action preparation slows the subjective passage of time. *Proc. Biol. Sci.* **279**, 4399–4406 (2012).
35. Yarrow, K., Haggard, P., Heal, R., Brown, P. & Rothwell, J. C. Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. *Nature* **414**, 302–305 (2001).
36. Morrone, M. C., Ross, J. & Burr, D. Saccadic eye movements cause compression of time as well as space. *Nat. Neurosci.* **8**, 950–954 (2005).
37. Haggard, P., Clark, S. & Kalogeras, J. Voluntary action and conscious awareness. *Nat. Neurosci.* **5**, 382–385 (2002).
This paper was the first to describe the intentional binding effect, in which the perceptions of a voluntary action and its outcome are shifted towards each other across time, introducing a novel implicit measure of sense of agency.
38. Caspar, E. A., Cleeremans, A. & Haggard, P. The relationship between human agency and embodiment. *Conscious. Cogn.* **33**, 226–236 (2015).
39. de Biran, P. M. *The Influence of Habit on the Faculty of Thinking* (The Williams & Wilkins company, 1929).
40. Moore, J. W., Wegner, D. M. & Haggard, P. Modulating the sense of agency with external cues. *Conscious. Cogn.* **18**, 1056–1064 (2009).
41. Ganos, C. *et al.* Volitional action as perceptual detection: predictors of conscious intention in adolescents with tic disorders. *Cortex* **64**, 47–54 (2015).
42. Shibasaki, H. & Hallett, M. What is the Bereitschaftspotential? *Clin. Neurophysiol.* **117**, 2341–2356 (2006).
43. Schurger, A., Sitt, J. D. & Dehaene, S. An accumulator model for spontaneous neural activity prior to self-initiated movement. *Proc. Natl Acad. Sci. USA* **109**, E2904–E2913 (2012).
This recent paper offered a radical reappraisal of the classical readiness potential, interpreting it as the average of a stochastic process of approaching a motor threshold rather than a specific motor signal.
44. Jo, H.-G., Wittmann, M., Hinterberger, T. & Schmidt, S. The readiness potential reflects intentional binding. *Front. Hum. Neurosci.* **8**, 421 (2014).
45. Haggard, P. & Clark, S. Intentional action: conscious experience and neural prediction. *Conscious. Cogn.* **12**, 695–707 (2003).
46. Barlas, Z. & Obhi, S. S. Freedom, choice, and the sense of agency. *Front. Hum. Neurosci.* **7**, 514 (2013).
47. Fletcher, P. C., Shallice, T. & Dolan, R. J. 'Sculpting the response space' — an account of left prefrontal activation at encoding. *Neuroimage* **12**, 404–417 (2000).
48. Rowe, J. B., Hughes, L. & Nimmo-Smith, I. Action selection: a race model for selected and non-selected actions distinguishes the contribution of premotor and prefrontal areas. *Neuroimage* **51**, 888–896 (2010).
49. Brass, M. & Haggard, P. The what, when, whether model of intentional action. *Neuroscientist* **14**, 319–325 (2008).
50. Rae, C. L., Hughes, L. E., Weaver, C., Anderson, M. C. & Rowe, J. B. Selection and stopping in voluntary action: a meta-analysis and combined fMRI study. *Neuroimage* **86**, 381–391 (2014).
51. Khalighinejad, N., Di Costa, S. & Haggard, P. Endogenous action selection processes in dorsolateral prefrontal cortex contribute to sense of agency: a meta-analysis of tDCS studies of 'intentional binding'. *Brain Stimul.* **9**, 372–379 (2016).
This paper showed that, across seven experiments and more than 100 participants, anodal stimulation of the PFC boosted the intentional binding effect in free-selection action tasks, which is consistent with the view that action-selection processes contribute prospectively to sense of agency.
52. Hughes, G., Desantis, A. & Waszak, F. Attenuation of auditory N1 results from identity-specific action-effect prediction. *Eur. J. Neurosci.* **37**, 1152–1158 (2013).
53. Schlaghecken, F. & Eimer, M. Masked prime stimuli can bias 'free' choices between response alternatives. *Psychon. Bull. Rev.* **11**, 463–468 (2004).
54. Wenke, D., Fleming, S. M. & Haggard, P. Subliminal priming of actions influences sense of control over effects of action. *Cognition* **115**, 26–38 (2010).
55. Chambon, V. & Haggard, P. Sense of control depends on fluency of action selection, not motor performance. *Cognition* **125**, 441–451 (2012).
56. Blakemore, S. J., Wolpert, D. & Frith, C. Why can't you tickle yourself? *Neuroreport* **11**, R11–R16 (2000).
This paper provided classical human behavioural evidence for a comparator model of agency, suggesting that predicted consequences of an action are subtracted from the actual consequences, resulting in attenuation of one's own agency.
57. Blakemore, S. J., Wolpert, D. M. & Frith, C. D. Central cancellation of self-produced tickle sensation. *Nat. Neurosci.* **1**, 635–640 (1998).
58. Farrer, C. & Frith, C. D. Experiencing oneself versus another person as being the cause of an action: the neural correlates of the experience of agency. *Neuroimage* **15**, 596–603 (2002).
59. Stetson, C., Cui, X., Montague, P. R. & Eagleman, D. M. Motor-sensory recalibration leads to an illusory reversal of action and sensation. *Neuron* **51**, 651–659 (2006).
60. Walsh, E. & Haggard, P. Action, prediction, and temporal awareness. *Acta Psychol. (Amst.)* **142**, 220–229 (2013).
61. Williams, S. R., Shenasa, J. & Chapman, C. E. Time course and magnitude of movement-related gating of tactile detection in humans. I. Importance of stimulus location. *J. Neurophysiol.* **79**, 947–963 (1998).
62. Bays, P. M., Flanagan, J. R. & Wolpert, D. M. Attenuation of self-generated tactile sensations is predictive, not postdictive. *PLoS Biol.* **4**, e28 (2006).
63. Reznik, D., Henkin, Y., Levy, O. & Mukamel, R. Perceived loudness of self-generated sounds is differentially modified by expected sound intensity. *PLoS ONE* **10**, e0127651 (2015).
64. Miall, R. C., Weir, D. J., Wolpert, D. M. & Stein, J. F. Is the cerebellum a smith predictor? *J. Mot. Behav.* **25**, 203–216 (1993).
65. Wegner, D. M. *The Illusion of Conscious Will* (MIT Press, 2002).
This masterful monograph from the greatly missed Harvard social psychologist contains a well-argued exposition of the argument that volition is an illusion and that our sense of being the authors of our own actions is a retrospective inference.
66. Aarts, H., Custers, R. & Wegner, D. M. On the inference of personal authorship: enhancing experienced agency by priming effect information. *Conscious. Cogn.* **14**, 439–458 (2005).
67. Gentsch, A. & Schutz-Bosbach, S. I did it: unconscious expectation of sensory consequences modulates the experience of self-agency and its functional signature. *J. Cogn. Neurosci.* **23**, 3817–3828 (2011).
68. Moore, J. & Haggard, P. Awareness of action: Inference and prediction. *Conscious. Cogn.* **17**, 136–144 (2008).
69. Eagleman, D. M. & Sejnowski, T. J. Motion integration and postdiction in visual awareness. *Science* **287**, 2036 (2000).
70. Farrer, C. *et al.* Modulating the experience of agency: a positron emission tomography study. *Neuroimage* **18**, 324–333 (2003).
71. Kincade, J. M., Abrams, R. A., Astafiev, S. V., Shulman, G. L. & Corbetta, M. An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. *J. Neurosci.* **25**, 4593–4604 (2005).
72. Craig, A. D. B. How do you feel — now? The anterior insula and human awareness. *Nat. Rev. Neurosci.* **10**, 59–70 (2009).
73. Chambon, V., Wenke, D., Fleming, S. M., Prinz, W. & Haggard, P. An online neural substrate for sense of agency. *Cereb. Cortex* **23**, 1031–1037 (2013).
74. Eimer, M. & Schlaghecken, F. Response facilitation and inhibition in subliminal priming. *Biol. Psychol.* **64**, 7–26 (2003).
75. Chambon, V., Moore, J. W. & Haggard, P. TMS stimulation over the inferior parietal cortex disrupts prospective sense of agency. *Brain Struct. Funct.* **220**, 3627–3639 (2015).
76. Cavazzana, A., Penolazzi, B., Begliomini, C. & Bisiacchi, P. S. Neural underpinnings of the 'agent brain': new evidence from transcranial direct current stimulation. *Eur. J. Neurosci.* **42**, 1889–1894 (2015).
77. Moore, J. W., Ruge, D., Wenke, D., Rothwell, J. & Haggard, P. Disrupting the experience of control in the human brain: pre-supplementary motor area contributes to the sense of agency. *Proc. R. Soc. B* **277**, 2503–2509 (2010).
78. Bratman, M. E. *Intention, Plans, and Practical Reason* (Cambridge Univ. Press, 1999).
79. Desmurget, M. & Sirigu, A. A parietal-premotor network for movement intention and motor awareness. *Trends Cogn. Sci.* **13**, 411–419 (2009).
80. Alloy, L. B. & Abramson, L. Y. Judgment of contingency in depressed and nondepressed students: sadder but wiser? *J. Exp. Psychol. Gen.* **108**, 441–485 (1979).
81. Frith, C. D., Blakemore, S. & Wolpert, D. M. Explaining the symptoms of schizophrenia: abnormalities in the awareness of action. *Brain Res. Brain Res. Rev.* **31**, 357–363 (2000).
82. Synofzik, M., Thier, P., Leube, D. T., Schlotterbeck, P. & Lindner, A. Misattributions of agency in schizophrenia are based on imprecise predictions about the sensory consequences of one's actions. *Brain* **133**, 262–271 (2010).
83. Daprati, E. *et al.* Looking for the agent: an investigation into consciousness of action and self-consciousness in schizophrenic patients. *Cognition* **65**, 71–86 (1997).
84. Blakemore, S. J., Smith, J., Steel, R., Johnstone, C. E. & Frith, C. D. The perception of self-produced sensory stimuli in patients with auditory hallucinations and passivity experiences: evidence for a breakdown in self-monitoring. *Psychol. Med.* **30**, 1131–1139 (2000).
85. Shergill, S. S., Samson, G., Bays, P. M., Frith, C. D. & Wolpert, D. M. Evidence for sensory prediction deficits in schizophrenia. *Am. J. Psychiatry* **162**, 2384–2386 (2005).
86. Shergill, S. S. *et al.* Functional magnetic resonance imaging of impaired sensory prediction in schizophrenia. *JAMA Psychiatry* **71**, 28–35 (2014).
87. Haggard, P., Martin, F., Taylor-Clarke, M., Jeannerod, M. & Franck, N. Awareness of action in schizophrenia. *Neuroreport* **14**, 1081–1085 (2003).
88. Waters, F. & Jablensky, A. Time discrimination deficits in schizophrenia patients with first-rank (passivity) symptoms. *Psychiatry Res.* **167**, 12–20 (2009).
89. Voss, M. *et al.* Altered awareness of action in schizophrenia: a specific deficit in predicting action consequences. *Brain* **133**, 3104–3112 (2010).
This paper used a simple experimental manipulation to dissociate the component of sense of agency based on retrospective inference from that based on outcome prediction; patients with schizophrenia relied more on the former, and healthy volunteers more on the latter.
90. Moore, M. S. *Law and Psychiatry: Rethinking the Relationship* (Cambridge Univ. Press, 1984).
91. Milgram, S. Behavioral study of obedience. *J. Abnorm. Psychol.* **67**, 371–378 (1963).
92. Caspar, E. A., Christensen, J., Cleeremans, A. & Haggard, P. Coercion changes the sense of agency in the human brain. *Curr. Biol.* **26**, 585–592 (2016).
This recent study combined an implicit measure of sense of agency with Milgram's classical obedience paradigm to show how coercive instructions reduce sense of agency over action outcomes.
93. Engbert, K., Wohlschlager, A. & Haggard, P. Who is causing what? The sense of agency is relational and efferent-triggered. *Cognition* **107**, 693–704 (2008).
94. Wegner, D. M. & Sparrow, B. in *The Cognitive Neurosciences* 3rd edn (ed. Gazzaniga, M.) 1201–1209 (MIT Press, 2004).
95. Lacey, N. Responsibility without consciousness. *Oxford J. Legal Studies* **35**, 665–696 (2015).

96. Libet, B., Gleason, C. A., Wright, E. W. & Pearl, D. K. Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). The unconscious initiation of a freely voluntary act. *Brain* **106**, 623–642 (1983).
97. DPP v. Camplin *[1978] (UKHL 2)* www.bailii.org http://www.bailii.org/uk/cases/UKHL/1978/2.html (1978).
98. Casey, B. J., Jones, R. M. & Hare, T. A. The adolescent brain. *Ann. NY Acad. Sci.* **1124**, 111–126 (2008).
99. Rex v. Kiranjit Ahluwalia [1992] EWCA Crim 1 www.bailii.org http://www.bailii.org/ew/cases/EWCA/Crim/1992/1.html (1993).
100. Abramson, L. Y., Seligman, M. E. & Teasdale, J. D. Learned helplessness in humans: critique and reformulation. *J. Abnorm. Psychol.* **87**, 49–74 (1978).
101. Coroners and Justice Act. 2009 section 52. Partial defence to murder: diminished responsibility www.legislation.gov.uk http://www.legislation.gov.uk/ukpga/2009/25/section/52 (2009).
102. Maier, S. F. & Watkins, L. R. Role of the medial prefrontal cortex in coping and resilience. *Brain Res.* **1355**, 52–60 (2010).
103. Kaye, K. & Fogel, A. The temporal structure of face-to-face communication between mothers and infants. *Dev. Psychol.* **16**, 454–464 (1980).
104. Ruvolo, P., Messinger, D. & Movellan, J. Infants time their smiles to make their moms smile. *PLoS ONE* **10**, e0136492 (2015).
105. Cipriani, D. *Children's Rights and the Minimum Age of Criminal Responsibility: A Global Perspective* (Ashgate Pub., 2009).
106. Brown, C. *My Left Foot* (Simon & Schuster, 1955).
107. Taylor, A. H. *et al.* Of babies and birds: complex tool behaviors are not sufficient for the evolution of the ability to create a novel causal intervention. *Proc. Biol. Sci.* **281**, 20140837 (2014).
108. Iriki, A. & Taoka, M. Triadic (ecological, neural, cognitive) niche construction: a scenario of human brain evolution extrapolating tool use and language from the control of reaching actions. *Phil. Trans. R. Soc. B* **367**, 10–23 (2012).
109. Iriki, A., Tanaka, M., Obayashi, S. & Iwamura, Y. Self-images in the video monitor coded by monkey intraparietal neurons. *Neurosci. Res.* **40**, 163–173 (2001).
110. Hochberg, L. R. *et al.* Neuronal ensemble control of prosthetic devices by a human with tetraplegia. *Nature* **442**, 164–171 (2006).
111. Koralek, A. C., Jin, X., Long, J. D., Costa, R. M. & Carmena, J. M. Corticostriatal plasticity is necessary for learning intentional neuroprosthetic skills. *Nature* **483**, 331–335 (2012).

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Competing interests statement

The author declares no competing interests.