in a nearly complete overthrow of the seedless vascular plants, which once dominated the planet. The modern-day descendants of these giants, still dependent on water for half of their life cycle, are almost exclusively confined to swampy or tropical habitats. *Equisetum*, with their highly proliferative and resilient rhizomes, are more versatile than many species and can be found in various environments.

How do humans use* Equisetum*?

In many cultures, the rough stems of horsetails are dried and used to scour and polish metal pots and pans, earning them the name 'scouring rush' in some parts of the world. In addition, traditional Japanese woodworkers use dried *Equisetum* as a type of extra-fine sandpaper. Since *Equisetum* species can be found all over the globe (except Australasia), they have made their way into the traditional medicine practices of various cultures, dating back to ancient Greek and Roman times. The silica in the stems of horsetails is thought to aid in osteoporosis prevention, while extracts from horsetails are used for many different reasons, including as a diuretic, and as a source of natural antioxidants. Very few studies, though, have been performed to weigh the merit of these alternative medical uses for the plant. Interestingly, livestock have been known to become ill and even die after eating large quantities of *Equisetum* — for this reason, and because most commercial pesticides kill only seed-bearing plants, horsetails are considered to be tricky pests in some areas.

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Sense of agency

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What is the sense of agency? The term 'sense of agency' refers to the experience of controlling one's own actions, and, through them, events in the outside world. Most of us have the feeling that we are in control of what we are doing most of the time: this is the normal sense of agency.

Why is it important? Some many mental illnesses involve abnormalities of agency: psychotic patients sometimes report that their actions are not their own, but are imposed on them by some other agent, while depressed patients often experience helplessness and loss of agency. Sense of agency also plays an important role in society generally, because it is central to the idea of responsibility for our own actions. In many countries, the law requires that a person be aware of the consequences of their actions, if they are to be found guilty of a crime.

How can sense of agency be studied scientifically? Despite its importance, sense of agency has proved difficult to study scientifically. Loss of agency, for example when one is driving a car that suddenly malfunctions, is a salient, and dramatic experience. But the normal flow of action and control forms a continuous, thin background to consciousness, rather than a specific, identifiable experience. Psychology and neuroscience have struggled to measure sense of agency. Most studies have used explicit agency attribution tasks, in which a person judges whether they did or did not cause a specific event. One experimental paradigm, for example, involves participants moving a joystick, while watching video feedback. They judge whether they caused the joystick movement shown on the video or not, equivalent to evaluating the truth or falsity of the proposition "I did that". These studies have shown that spatial and temporal contiguity between one's own and the observed movement are the major cues for self-attributing agency; however, they say little about the *phenomenology* or experience of agency: that is, what it feels like to be in control of the image viewed on the screen, as opposed to out of control.

What brain computations underlie sense of agency? The experiments described above suggest the brain computes agency by predicting the consequences of current actions, and comparing these predictions to actual outcomes (Figure 1A). In the example above, knowing how one moves the joystick allows one to predict the visual feedback. If the video feedback matches the prediction, then it follows that "I did that". If there is no match, then the visual feedback must have another cause. This account is based on the computations used to monitor and adjust motor commands in a popular computational framework for action control, leading to the suggestion that sense of agency is simply the normal operation of the goal-directed action system (Farrer *et al*. 2008). In this framework, agency is computed by comparing a prospective signal (the intention or command to achieve the goal) and a retrospective signal (the actual feedback or outcome of action). An internal forward model uses a copy of the current motor command to predict the feedback that the action will produce. If the comparison between predicted and actual feedback generates no error, then "I did that".

Brain imaging studies of such tasks have not found any clear positive correlate of agency, but routinely show activation of the angular gyrus in the parietal cortex in situations of non-agency. Angular gyrus activation increases proportionately as the subjective sense of agency decreases. This brain area may therefore either house the comparator, or receive the error signals transmitted by a comparator located somewhere else in the brain. These studies suggest a strong link between sense of agency and error-monitoring in the motor control system, but they leave two important questions unanswered. First, why do we have a positive sense of agency, in addition to the negative sense of non-agency that occurs when the outcome of an action is not as predicted? Second, what experience is there prior to receiving delayed feedback about action outcomes: could an experience similar to agency

be present at the time of the action itself, or even before it?

When does the brain compute the sense of agency? Most recent studies emphasise the *retrospective* component of agency for two reasons. First, the outcome of actions can be readily manipulated experimentally, but there are few methods for studying intentions. Second, psychological experiments have shown that we are often mistaken about our own intentions. For example, in an experiment where the outcomes of participants' action choices were surreptitiously changed, participants reported having an intention corresponding to the actual outcome, rather than their original choice (Johansson *et al*. 2005). On one extreme view, sense of agency is really a retrospective confabulation to explain our own action choices, rather than a direct experiential consequence of neural processing in the brain's motor systems. The predictions generated by forward models in the motor system may not reach conscious awareness.

There are, however, several reasons for thinking that sense of agency strongly depends on prospective processes, and is not just a retrospective confabulation. First, the brain prospectively represents the outcomes of actions *before* action occurs. Prior information about action outcomes increases sense of agency over those outcomes. When people are shown subliminal prime stimuli just prior to an action, primes corresponding to the consequences of the impending action lead to a stronger experience of control over the outcome than non-corresponding primes. The primes in these experiments are not consciously perceived, but are assumed to boost the representation of the action outcome.

Could sense of agency be a metacognitive experience based on action selection? Recent studies have suggested that the brain processes that select between alternative actions may provide a second prospective agency signal, in addition to those generated by predicting action outcomes. Specifically, people feel a stronger sense of control when they choose fluently and easily what to do (Wenke *et al.* 2010). This finding

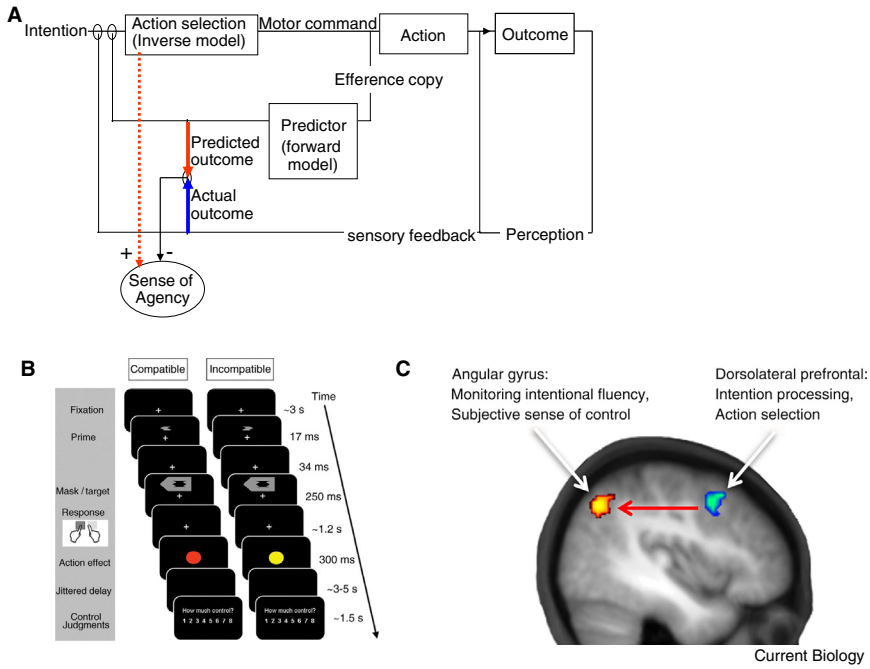

Figure 1. The sense of agency.
(A) Computational motor control frameworks and sense of agency. To achieve a given intention or goal, an inverse model selects an appropriate motor command. The forward model predicts the outcome of the motor command, and this is compared to the actual outcome reported by sensory feedback. A comparator matches prospective signals (red arrows) and retrospective signals (blue arrow). Zero comparator error corresponds to a sense of agency. A second prospective signal generated during action selection directly contributes to the sense of agency (dashed red arrow). Easy and fluent selection of the appropriate action leads to stronger sense of agency. (B) Subliminal priming influences sense of agency over action outcomes. Participants make left or right keypresses in response to target arrows. Brief subliminal arrow primes precede these targets, and can be either compatible or incompatible with the action indicated by the target. Keypress responses to the target elicit one of several colour patches, after a variable delay. Participants report more control over the colour patch on compatibly-primed trials, compared to incompatibly primed trials. (C) A possible circuit for prospective agency. Dorsolateral prefrontal cortex selects between alternative possible actions. Conflict signals from this area are monitored by the angular gyrus, where they are interpreted as a reduced sense of control. Adapted from Chambon *et al*. (2012).

suggests that the sense of agency depends on volitional processes that necessarily precede action, and so cannot be purely retrospective. In one study (Figure 1B), people were instructed whether to press a key with the left or right hand, or else freely chose which hand to press with. Subliminal arrow primes just before these instructions could either facilitate or interfere with these choices, by making action selection more or less fluent. Each action had the effect of making a colour appear on the screen. Importantly, different colour effects were used on trials where the primes were compatible with the instructed or freely-chosen response, and on trials where the primes were incompatible. Importantly, the colour effects did not depend on the primes themselves, but on the relation between prime and subsequent action. After several trials, participants rank-ordered how much control they felt over the different colour effects they experienced. They reported stronger sense of agency over colours that followed compatibly-primed actions rather than incompatibly-primed actions, irrespective of whether they freely choose between actions, or were instructed which action to make.

How might action selection influence sense of agency? Most people recognise situations where they know exactly what to do, and fluently select the next appropriate action, like a well-trained pilot in an emergency. These situations seem to produce a strong sense of agency, even before the outcome of action is known. Subliminal priming of actions may capture this situation experimentally.

Our recent brain imaging study (Chambon *et al*. 2012) found evidence that the interaction between the angular gyrus of the parietal cortex, and the action selection centres in the prefrontal cortex, plays a key role in the prospective sense of agency. When incompatible primes interfered with the decision of which action to make, the angular gyrus activation at the time of action selection showed a negative correlation with sense of agency over action outcome. This negative correlation had been observed before, and was explained in terms of prediction-outcome matching. In contrast, our study found that angular gyrus might compute non-agency at the time of action selection, and not just retrospectively once outcomes were known. This study found no relation between angular gyrus activation and sense of control on compatibly-primed trials, suggesting that this area monitors a signal related to difficulty and conflict during action selection, rather than the normal smooth flow of agency (Figure 1C).

Moreover, the lateral prefrontal cortex, which is responsible for selecting between different possible actions, showed a negative correlation with the angular gyrus activation on incompatibly-primed only, and no correlation on compatibly-primed trials. These findings suggest a new model, in which sense of agency depends as much on how we choose what we do, as on actually doing it. The positive sense of agency, or feeling in control, could reflect the default state of the brain's action selection networks, while the feeling of loss of control could reflect angular gyrus monitoring the conflict within frontal action selection mechanisms. On this view, the experience of agency would be a form of 'metacognition', or conscious experience corresponding to efficiency of action selection. In the computational framework above, the planner process, or inverse model, must contribute to the sense of agency, as well as the match between forward model prediction and outcome.

Why do we have a conscious experience of agency? The prospective aspect of agency gives a clue as to *why* the brain might provide a distinctive conscious experience of being in control. Selecting between alternative action choices is often a difficult computational problem for the brain. An experience of sense of agency corresponding to fluent choice may be an important signal for guiding these computations. For example, we often make errors by pressing the wrong button on a machine, or by not knowing which button to press. The prospective sense of agency may be the brain's way of generating the feeling of "just knowing the right button to press". In contrast, prospective feelings of non-agency may allow time to slow down, perhaps switching the brain to a more attentive strategy of supervisory control. It is clearly useful to have such feelings prospectively, *before* pressing the wrong button, yet existing comparator models can only explain the retrospective feeling of error *after* one has pressed the wrong button. The prospective sense of agency may serve as a marker when action processing needs to shift from routine to supervisory control.

We saw above that retrospective sense of agency can be tricked, and is sometimes illusory. The prospective sense of agency may also be an illusion. Simply having a feeling of fluently knowing which action to select does not guarantee the correct action outcome. For example, I may clearly feel that I know which button to press on the machine, but I may actually press the wrong button, or the machine may malfunction. The prospective sense of agency might only develop once the brain has learned a stable relation between actions and outcomes.

Where can I find out more?

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Primer

Qualia

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Perhaps the most difficult biological question of all might be how and why electrochemical neuronal activity in the brain generates subjective conscious experience such as the redness of red or the painfulness of pain. Neuroscientists track how light impinging on the retina is transformed into electrical pulses (neuronal spikes), relayed through the visual thalamus to reach the visual cortex, and finally culminates in activity within speech-related areas causing us to say 'red'. But how such experience as the redness of red emerges from the processing of sensory information is utterly mysterious. It is also unclear why these experiences possess phenomenal characteristics, which can be directly accessed only from the subject having the experience. This is called the 'hard problem' of consciousness as coined by the philosopher David Chalmers. The phenomenal aspect of consciousness or 'what it is like' character of subjective experience is called 'qualia'; the singular form of the word is 'quale', from the Latin for 'what sort' or 'what kind'. In this Primer, we provide an overview of the term 'qualia' and its conceptual issues, and how neurobiological approaches can contribute to clarify some of these issues.

The difficulty with qualia is their subjective nature: qualia exist only as viewed from the inside. They cannot be objectively detected or compared like any other properties measured in natural sciences. The subjectivity of qualia allows one to conceive hypothetical situations that philosophers discuss in thought experiments. For instance, we can assume, without any contradiction, a person with *inverted qualia* who, when seeing the colour red, has the quale that you would have when seeing the colour green, and conversely. In another thought experiment we can conceive a *philosophical zombie* who has all the cognitive and perceptual abilities like us but lacks any phenomenal experience. These thought experiments are often