How Does Neuroscience Affect Our Conception of Volition?

Adina L. Roskies

Department of Philosophy, Dartmouth College, Hanover, New Hampshire 03755;
email: adina.roskies@dartmouth.edu

Annu. Rev. Neurosci. 2010. 33:109–30

The *Annual Review of Neuroscience* is online at neuro.annualreviews.org

This article's doi:
10.1146/annurev-neuro-060909-153151

0147-006X/10/0721-0109$20.00

Key Words

free will, decision, intention, control, agency, determinism

Abstract

Although there is no clear concept of volition or the will, we do have intuitive ideas that characterize the will, agency, and voluntary behavior. Here I review results from a number of strands of neuroscientific research that bear upon our intuitive notions of the will. These neuroscientific results provide some insight into the neural circuits mediating behaviors that we identify as related to will and volition. Although some researchers contend that neuroscience will undermine our views about free will, to date no results have succeeded in fundamentally disrupting our commonsensical beliefs. Still, the picture emerging from neuroscience does raise new questions, and ultimately may put pressure on some intuitive notions about what is necessary for free will.

Contents

INTRODUCTION

Long a topic of debate for theologians and philosophers, the will, or the faculty of volition, was an object of scientific study for psychologists of the nineteenth century. Volition fell off the scientific radar screen with the behaviorist revolutions in philosophy and psychology, for the will was deemed too thoroughgoing a mentalistic concept to be amenable to empirical approaches. However, with the more recent abandonment of dualistic perspectives and the development of novel techniques for investigating the brain, the topic of volition is enjoying something of a renaissance. Discussions of freedom of the will in philosophy are also blossoming, and much of the impetus for volition's resurrection lies in the new challenges and opportunities posed by the cognitive and neural sciences (see sidebar, The Philosophy of Free Will).

Volition: the faculty that makes possible voluntary action or choice; the will

Intention: mental states representing plans for future action. There may be many kinds of intention

Phenomenology: what an experience is like from the perspective of the subject

PHILOSOPHICAL AND EXPERIMENTAL APPROACHES TO VOLITION

There is no uncontroversial, univocal concept of volition to be found in philosophy or in the sciences (Audi 1993; Brass & Haggard 2008; Zhu 2004a,b). Generally speaking, volition is a construct used to refer to the ground for endogenous action, autonomy, or choice. Intuitions vary on the specifics: Some contrast voluntary actions with actions that are reflexive or specified by the environment; others claim that the will is primarily involved in making decisions that then determine action; still others combine these views in holding that choices are but mental acts. Volition is sometimes used to refer to the endogenous mental act of deciding or forming an intention (Searle 1983, Zhu 2004a); at other times it is used to refer to the decision or intention itself (Adams & Mele 1992). Some suggest that volition is independent of the successful execution of the willed act itself, and that a central aspect of volition lies in the trying (Adams & Mele 1992).

The heterogeneity of the preceding list provides one clue to the difficulties in reviewing the impact of neuroscience on our conception of volition, for the absence of a clear concept of volition complicates the task of investigating it experimentally. In addition, in order for neuroscientific research to bear upon the conception of volition, volition has to be operationalized in some way. In light of these considerations, I organize my discussion around five different experimental threads which, separately or in combination, seem to capture much of what is signified by the intuitive, but less than clear, concept of the will. These threads are (*a*) initiation of action, (*b*) intention, (*c*) decision, (*d*) inhibition and control, and (*e*) phenomenology of agency. These five themes map loosely onto Haggard & Brass' (2008) "What, when, whether" model of intentional action.

There are relatively identifiable bodies of research associated with each of the above themes, although many of them blend into each other. Moreover, each of these maps to some elements of the commonsensical conceptions of volition. For example, if one takes voluntary action to contrast with stimulus-generated action, examining the neural events that distinguish self-initiated movements from similar movements that are responses to external stimuli ought to provide insight into the proximal mechanisms underlying endogenously generated action.

However, if one conceives of volition as not essentially tied to motor movements, but rather to abstract plans for future action, the proximal mechanisms that lead to simple movements may be of less interest than the longer-term plans or intentions one has or forms. Some research on intentions attempts to address these higher-level aspects of motor planning. Philosophical discussions of volition often focus upon the ability to choose to act in one way or another. Although historically this emphasis on choice may be a vestige of an implicit dualism between the mentalism of choice and the physicalism of action, the processes underlying decision as a means for forming intentions seem to be a central aspect of volition even if one rejects dualism, as most contemporary philosophers and scientists have.

A different approach to volition focuses less on the prospective influence of the will on future action than on the occurrent ability of the subject to inhibit or control action. Although one might not intuitively think of control as central to the will, recognizing the importance of control for attributions of responsibility in morality and the law may help clarify the relevance of control to volition. Moreover, some lines of evidence from psychology and neuroscience suggest that actions are often initiated unconsciously (e.g., Libet 1985), and so if free will is to exist, it will take the form of control or veto power over unconsciously initiated actions. Finally, regardless of whether one believes that we can act or choose freely, we normally do perceive certain actions as self-caused and others as not. Most people concur that there is phenomenology that accompanies voluntary action, and neuroscience has begun to illuminate the physiological basis of the feeling of agency.

Work on these five strands thus may influence or illuminate our conception of volition. A few caveats are in order before we begin. First, in light of the lack of agreement about the concept of volition itself, and its close relation to discussions of the will and of agency, I feel free to use the terms volition, will, and agency interchangeably, without, I hope, additionally muddying the waters. That is not to say that there are not substantive distinctions to be made between them. Second, because of the extensive literature in each of the areas discussed, I focus more on discussions of how neuroscience has, can, or may affect our conception of volition, rather than on an exhaustive review of the literature in each of these lines of research. Finally, I recognize that there is a considerable literature on the neural basis of perceiving and attributing agency to others (Ciaramidaro et al. 2007, Cunnington et al. 2006, de Lange et al. 2008, Fogassi et al. 2005, Hamilton & Grafton 2006, Ramnani & Miall 2004, Rizzolatti & Sinigaglia 2007). On some hypotheses, the neural systems that support perception of agency in others are the same as those operative in perception of self-agency (Ciaramidaro et al. 2007, Cunnington et al. 2006, Fogassi et al. 2005, Iacoboni et al. 2005, Lamm et al. 2007, Rizzolatti & Sinigaglia

THE PHILOSOPHY OF FREE WILL

Philosophers have typically framed the problem of free will in terms of determinism and indeterminism. Compatibilists try to provide accounts of freedom that are compatible with determinism; incompatibilists deny that we can be free if determinism is true. Incompatibilists come in two flavors: Hard determinists place their bet on the side of determinism's truth, and deny that we are free; Libertarians maintain that we are free in virtue of indeterministic events. The challenge for the compatibilist is to show how we can be free or morally responsible if we could not act otherwise than we do. The Libertarian's challenge is to make his picture scientifically plausible, while showing how indeterministic events can have the right connection to choice and action to confer agency and responsibility.

Traditionally, freedom is thought to be intimately tied to moral responsibility. Now, however, some philosophers try to dissociate moral responsibility from freedom; others suggest that mechanistic explanation of the causes of behavior, not determinism, poses the greatest threat to freedom and responsibility. These new angles on old philosophical questions, as well as scientific inroads into understanding the neural bases of behavior, make it an exciting time to contemplate the philosophy of free will.

Dualism: mental and physical belong to two fundamentally different ontological categories, and cannot be reduced to each other

2007). Although this literature may indirectly bear upon our understanding of volition, I do not discuss it here. Finally, this paper does not attempt to review the philosophical work regarding volition. I begin, however, with a brief digression on the relation between volition and freedom.

Determinism: the claim that every event is fully specified by the state of the universe and the natural laws; denial of truly random or probabilistic processes

Incompatibilists: those who believe that freedom is not compatible with determinism

Compatibilists: those who believe that freedom is compatible with determinism

VOLITION AND FREEDOM

It is difficult, if not impossible, to disentangle our notion of volition from questions about human freedom. The construct of volition largely exists in order to explain the possibility, nature, or feeling of autonomous agency. Before discussing the neuroscientific literature relating to volition, I want to say a few words about neuroscientific approaches that do not hold much promise for adjudicating the problem of free will.

In philosophy, discussions of freedom have traditionally hinged in part upon the question of how freedom relates to determinism, and in part on whether determinism is true. Incompatibilists believe that determinism precludes freedom, whereas compatibilists believe that determinism is compatible with, or even necessary for, freedom. Although the question of whether the universe (or the brain) is deterministic is a matter of empirical fact, it is not a fact that can be established by neuroscience. Some neuroscientists seem to think that neuroscientific work is able to illuminate the truth or falsity of determinism, by identifying the neural manifestation of indeterminism in randomness, noise, or stochastic behavior of neural systems. This, I believe, is mistaken, for at least two reasons. Although neuroscience may provide data that appear to reflect randomness or stochastic behavior in the nervous system, the epistemic limits of neuroscientific investigation are such that the evidence we gather from neuroscientific techniques is an insufficient basis from which to make that determination (Roskies 2006). Moreover, merely establishing randomness in the nervous system would be insufficient to account for human freedom: Randomness would have to be shown to play the right role in processes of volition for it to ground freedom.

Regarding the first point, in order for neuroscience to bear upon the truth or falsity of determinism, it has to have something to measure, and it does this by operationalizing determinism as predictability. However, predictability is at best a poor cousin to determinism, and one that can betray its familial roots. Although a deterministic system is in principle predictable, in practice predictability is not a guide to determinism. What appears to be stochastic behavior at one level could be the result of deterministic processes at a lower level. For example, Mainen & Sejnowski (1995) found that spike timing that appeared to be stochastic with the injection of DC current was in fact extremely reliable when neurons were injected with the same variable voltage patterns that characterized their normal inputs. This finding might suggest that neuronal firing operates deterministically (but see Dorval 2006). However, the Mainen & Sejnowski data indicated that although spike timing was remarkably reliable, it was not perfect. These discrepancies could be attributable to stochastic behavior, but also to entirely deterministic factors such as unmonitored inputs, or to other features of the neuron that varied between trials. Similar ambiguities arise when one looks at a finer grain. For example, the stochastic properties of neurotransmitter release may be due to fundamentally probabilistic processes, or to the purely deterministic operation of a system that is structurally variable over time at the subcellular level, such as the spatial distribution of vesicles in the presynaptic terminal (Franks et al. 2003). Thus, in order to make judgments about determinism from neuroscientific data, we would need to know far more about the microphysical makeup of neurons than our neurophysiological techniques tell us, as well as to have complete information about the global state of the system impinging upon the neurons from which we are recording.

While certain features of neural events may be signatures of random behavior (e.g., Poisson distributions), such features can also be generated by deterministic mechanisms (Glimcher 2005). For example, the "random" number generators in computers are merely deterministic algorithms, and many chaotic processes are deterministic. Although some neuroscientists seem to be convinced that neuronal behavior is indeterministic, the verdict is still out. References to noise in neural systems invoke the spirit of indeterminism, but one person's noise is another's signal. In the absence of a clear and complete understanding of the way the brain codes and reads out relevant information, we cannot simply label unexplained activity as noise and from there infer that brain processes are indeterministic in the sense required by the incompatibilist. That said, there may be ways to view the role of variability in neural activity as relevant to decision or action that do not hinge upon the question of determinism.

Neuroscience can affect views on free will by elucidating mechanisms underlying behavior (where mechanism is silent on the determinism question). Merely elucidating mechanism may affect the layperson's views on freedom (Monterosso et al. 2005, Nahmias et al. 2007), but on the assumption that dualism is false, mechanistic or causal explanation alone is insufficient for answering the question of freedom. The real interest lies in whether neuroscientific accounts show volition to have or lack characteristics that comport with our intuitive notions of the requirements for freedom of the will. When discussing the relevance that the neuroscientific data have for our belief in freedom of the will, I focus upon whether particular empirical characteristics of the will put pressure on ordinary notions of freedom.

NEUROSCIENTIFIC APPROACHES TO VOLITION

Volition as Initiation

The will is thought to be critical in endogenously generated or self-initiated actions, as opposed to exogenously triggered actions, like reflexes or simple stimulus-response associations. This view may be criticized on a number of fronts, among them that no such dichotomy in action types makes sense. Nevertheless, a number of neuroscientific studies have compared brain activity during self-initiated and externally cued actions, and have found differences in the functional architecture subserving actions that are externally cued and those that are not (Haggard 2008).

Imaging studies of endogenous generation of simple motor actions compared to rest consistently show activation of primary motor cortex, SMA (supplementary motor area) and preSMA, regions in the anterior cingulate, basal ganglia, and DLPFC (dorsolateral prefrontal cortex). Cued responses seem to involve a network including parietal and lateral premotor cortices that mediate sensory guidance of action.

Prior to the availability of imaging techniques, EEG recordings at the vertex revealed a slow negative electrical potential that precedes motor activity by 1–2 seconds (**Figure 1**). This "readiness potential" (RP) was initially hypothesized to arise in the SMA (Deecke & Kornhuber 1978, Jahanshahi et al. 1995). Further studies have suggested that the RP reflects more than one component process (Haggard & Eimer 1999, Libet et al. 1982, Shibasaki & Hallett 2006), and the source of the early components of the RP has been localized to preSMA (Shibasaki & Hallett 2006). The magnitude of the RP is greater in self-paced than in cued movements, and studies indicate that the late and peak phases of this electrical signal are associated with spontaneous or self-initiated motor acts, whereas the earliest components may be more involved in cognitive processes related to preparation or motivation (Jahanshahi et al. 1995, Libet et al. 1982, Trevena & Miller 2002).

Despite abundant evidence implicating medial frontal cortex in self-initiation of movements, determination of the source and function of the differences in brain activity during self-initiated and cued actions is a matter about which there is less consensus. A PET study controlling for predictability of movement timing suggests that the signals associated with

SMA: supplementary motor area

DLPFC: dorsolateral prefrontal cortex

Readiness potential (RP) or the Bereitschafts potential: an electrical negativity recorded at the midline with EEG that precedes voluntary movement

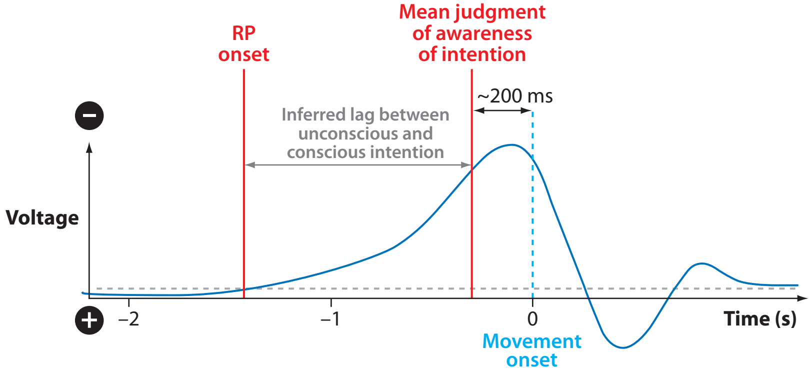

Figure 1

Schematic results of Libet's findings. On average, neural signals in the motor areas of the brain preceding finger movement (RP) begin more than 1 s before movement onset, whereas awareness of intending the movement, by contrast, is reported to be only ∼200 ms before movement onset. Reprinted from Haggard (2005). [Reprinted from Haggard (2005) with permission from Elsevier]

self-paced actions arise in the rostral SMA, anterior cingulate, and DLPFC (Jenkins et al. 2000). Using fMRI, Deiber et al. (1999) mapped results onto the medial frontal anatomical areas defined by Picard & Strick (1996) and found that activation in preSMA and rCZ (rostral cingulate zone) were greater in self-initiated than in externally cued movements. Cunnington et al. (2002) found a difference in the timing, but not level of activation in preSMA with self-paced movements, and also report activation in rCZ. Lau et al. (2004b) try to disentangle attention to selection of action from initiation, and find that preSMA, but not DLPFC, is preferentially activated during initiation. However, in this study the greater activity in this region is correlated with time on task, and thus may not reflect specificity for initiation. Mueller et al. (2007) argue that once other variables are controlled for, preSMA fails to show differences between self-initiated and cued movement tasks, and they associate self-initiated movements with activity in rCZ and not preSMA.

Lesions of the preSMA in the monkey inhibit self-initiation of action, but not cued action (Thaler et al. 1995). In humans, direct electrical stimulation of regions in the SMA (including preSMA) produces an urge to move; stronger stimulation results in action (Fried et al. 1991). In addition, rTMS (repetitive transcranial magnetic stimulation) of preSMA disrupts initiation of uncued motor sequences (Kennerley et al. 2004) during task switching. These studies provide further evidence of the involvement of these areas in action initiation. These regions also may be involved in automatic inhibition of competing responses: On the basis of unconscious priming studies with lesion patients, Sumner et al. (2007) report that SMA (but not preSMA) mediates automatic inhibition of motor plans in performance of alternative voluntary actions. Lesions in these regions prevent that inhibition (Sumner et al. 2007), and appear in some syndromes characterized by involuntary motor behavior (Haggard 2008).

In summary, the areas most consistently associated with action initiation are the rCZ and preSMA, but interpretation of their function is still controversial. A variety of factors make it difficult to reconcile results of many studies. Some paradigms require the subject to decide upon the timing of an instructed action, whereas others require choice between action alternatives. Reported results may reflect task confounds such as complexity of stimulus-action associations and conflict-induced activity rather than something particularly related to volition (Nachev et al. 2008). Indeed, there is some evidence that

rCZ: rostral cingulate zone

rTMS: repetitive transcranial magnetic stimulation preSMA and rCZ can be subdivided into subregions preferentially involved in response conflict and initiation (Nachev et al. 2005, Picard & Strick 2001). Future work will better resolve the regions involved in self-initiated and externally cued activity, and the circuits mediating such processing. These results may provide clearer targets for future experiments. However, until more is known about the computations involved, the precise identification of regions involved in self-initiation does little to influence our conception of volition.

Volition as Intention

Intentions are representational states that bridge the gap between deliberation and action. Arguably, intentions can be conscious or unconscious. Moreover, there may be different types of intention involved in different levels of planning for action (Pacherie 2006). If we assume that intentions are the proximal cause of all voluntary movement, then studies of initiation of action and of intention may well concern the same phenomena (we might call these proximal intentions or motor-intentions, or as some call them, volitions). However, we also commonly refer to intentions in a broader, more abstract sense, as standing states that constitute conscious or purposeful plans for future action, that exist prior to and independently of action execution. In moral and legal contexts, when we ask whether a person acted intentionally, we often employ this more general notion of intention.

In general, willed action involves the intention to act, and many presume that freely willed actions must be caused by our conscious intentions. The efficacy of our conscious intentions was challenged by the studies of Benjamin Libet, who examined the relative timing of awareness of the intention to move and the neural signals reflecting the initiation of action. Libet reported that the time of onset of the readiness potential (RP) occurs approximately 350 ms or more prior to the awareness of an urge or intention to move (Libet 1985; Libet et al. 1982, 1983b,c) (**Figure 1**). Libet and others have viewed this discrepancy as evidence that actions are not consciously initiated (see Banks 2002, Libet 1985, Libet et al. 1983a). Many have taken these results as a challenge to free will, on the supposition that conscious intention must drive, and thus precede, initiation of action for that action to be freely willed. Although Libet's basic neurophysiological findings about RP timing have withstood scrutiny (Haggard & Eimer 1999, Matsuhashi & Hallett 2008, Trevena & Miller 2002), his interpretations have been widely criticized. For example, Libet's data do not enable us to determine whether the RP is always followed by a movement, and thus whether it really reflects movement initiation, as opposed to a general preparatory signal or a signal related to intention (Mele 2006, Roskies 2010).Haggard & Eimer use temporal correlation to explore the possibility that the anticipatory brain processes identified by Libet and others underlie the awareness of intention. Their results suggest that a different signal, the lateralized readiness potential (LRP), is a better candidate than the RP for a brain process related to motor intention (Haggard & Eimer 1999). Trevena & Miller agree that the LRP is more closely tied to movement initiation than is the RP, and their data suggest that awareness of intention may precede the LRP. Others argue that Libet's experimental design fails to accurately measure the onset of conscious intention to move (Bittner 1996, Lau et al. 2006, Roskies 2010, Young 2006), and may measure a different state instead (Banks 2002). Other research suggests that the Libet paradigm may bias judgments of the time of conscious awareness (Lau et al. 2006, 2007), so that inferences about relative timing may not be reliable. (For further commentary on Libet, see Banks 2002, Banks & Pockett 2007, Mele 2009, Pacherie 2006, Sinnott-Armstrong & Nadel 2010.) In sum, Libet's studies do little to undermine the general notion of human freedom, even if they do suggest that in certain kinds of repetitive motion tasks, individual motor movements may not be consciously initiated.

LRP: lateralized readiness potential

BOLD: blood oxygenation level dependent

IPS: interparietal sulcus

PPC: posterior parietal cortex

In a recent event-related study probing the timing of motor intentions, Haynes and colleagues used pattern classification techniques on fMRI data from regions of frontopolar and parietal cortex to predict a motor decision. Surprisingly, information that aided prediction was available 7–10 seconds before the decision was consciously made, although prediction success prior to awareness was only slightly better than chance (~60%) (Soon et al. 2008). This study demonstrates that prior brain states, presumably unconscious, can influence or bias decision-making. While neural precursors to decision and action and physical influences on behavior are to be expected from cognitive systems that are physically embodied, it is startling that any brain information could provide much guidance to future arbitrary decisions so long before they are made. The weak predictive success of this study does not undermine our notion of volition or freedom, but it nonetheless raises important challenges to ordinary views about choice.

Little neuroscientific work has focused explicitly on abstract human intentions, in part because it is so difficult to figure out how to measure them objectively. In one study, Lau et al. (2004a) instructed subjects to press a button at will, while attending to the timing of either their intention to move, or the movement itself. Attention to intention led to increased BOLD (blood oxygenation level dependent) signal in pre-SMA, DLPFC, and IPS (interparietal sulcus) relative to attention to movement. Relying on a large body of imaging results indicating that attention to specific aspects of a cognitive task increases blood flow to regions involved in processing those aspects (Corbetta et al. 1990, O'Craven et al. 1997), they interpreted their results to indicate that motor intention is represented in the pre-SMA. These results are consistent with the view that proximal intentions leading to self-initiated motor activity are represented in the pre-SMA, but also with the view that conscious intentions are represented there as well.

In addition to pre-SMA, Lau's study highlighted frontal and parietal regions often implicated in intentional action (**Figure 2**). Hesse et al. (2006) identify a frontoparietal network in motor planning, including left supramarginal gyrus, IPS, and frontal regions. The left anterior IPS has also been associated with goal representation, crucial in motor planning (Hamilton & Grafton 2006). These results are consistent with the view that posterior parietal regions represent motor intentions (Andersen & Buneo 2003, Cui & Andersen 2007, Quian Quiroga et al. 2006, Thoenissen et al. 2002). Sirigu et al. (2004) report that damage to parietal cortex disrupts awareness of intention to act, although voluntary action is undisturbed. The role of PPC (posterior parietal cortex) in the experience of intention is further discussed in a later section.

Often we think of intentions as more abstract plans less closely related to motor activity. Many studies indicate that dorsal prefrontal cortex (DPFC) is active in tasks involving willed action. Medial parts of DPFC may be involved in thinking about one's own intentions (den Ouden et al. 2005), whereas DLPFC may be involved in generating cognitive as well as motor responses (Frith et al. 1991, Hyder et al. 1997, Jenkins et al. 2000, Lau et al. 2004a). However, it is difficult to determine whether the activity observed corresponds to selection, control, or attention to action. Lau et al. (2004b) attempt to control for working memory and attention in a free response task in order to determine what areas are involved in selection of action. DLPFC was not more active in the free choice than in the externally specified selection condition, suggesting it had more to do with attention to selection than with choice. In contrast, preSMA was more active in free choice than in other conditions. This provides further evidence that preSMA is involved in free selection of action. Moreover, attention to selection involves DLPFC. Since attention may be required for awareness of intention, DLPFC activity may reflect conscious intention.

Thus far, the regions discussed reveal little about the content of intentions. Using pattern-analysis on fMRI data from regions of prefrontal and parietal cortex, Haynes and

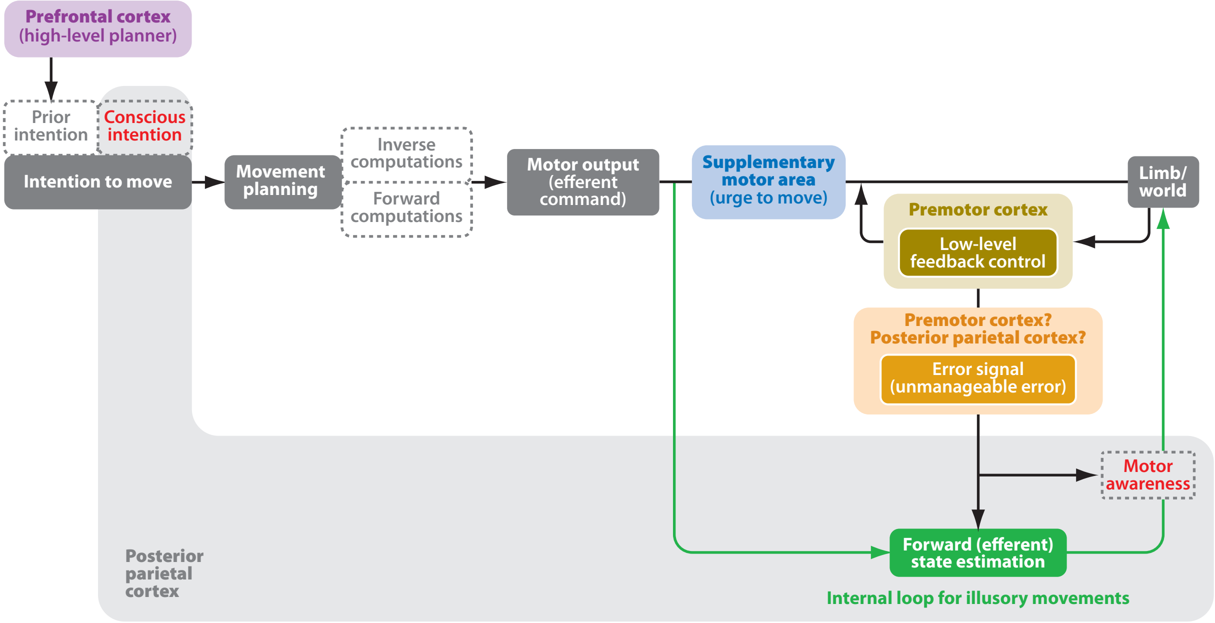

Figure 2

Partial schematic of information flow for voluntary action and awareness of agency, involving prefrontal, posterior parietal, and premotor cortices. Adapted from Desmurget & Sirigu (2009).

colleagues were able predict with up to 70% accuracy a subject's conscious but covert intention to add or subtract numbers (Haynes et al. 2007). Information related to specific intentions is thus present in these regions (including medial, lateral, and frontopolar prefrontal regions) while the subject holds his intended action in mind. Regions that are predictive appear to be distinct from the ones generally implicated in representation of intention or endogenous actions, raising the possibility that information related to intention is differentially represented depending on task.

To date, neuroscience has shown that mechanisms underlying endogenous initiation and selection of action have some features that deviate from commonsensical conceptions of volition, largely with regard to the relative timing of neural events and awareness. Although in certain contexts neural mechanisms of selection and motor intention may be unconsciously activated, once one takes into account the variety of levels at which intentions operate (Mele 2009, Pacherie 2006, Roskies 2010), none of the current data undermines the basic notions of volition or free will. Reports of the death of human freedom have been greatly exaggerated.

Volition as Decision-Making

In one prevalent view, the paradigmatic exercise of the will lies in our ability to choose what course of action to take, rather than to initiate or represent future action. Many philosophers have located freedom of the will in the ability to choose freely which intentions to form. Decision often precedes intention and initiation.

Researchers in primate neurophysiology are constructing a rich picture of the dynamics of perceptual decision-making, using single-cell recording and population modeling. Because of its cohesiveness and breadth I concentrate on a body of work from the laboratories of William Newsome, Michael Shadlen, and colleagues, who have elucidated in detail the neural basis of decision-making under uncertainty using a visual motion paradigm. This work has been extensively reviewed elsewhere (Glimcher

2001, 2003; Gold & Shadlen 2007); I briefly summarize the main findings here.

Saccade: an eye movement in which the eyes jump from one point in the visual field to another

LIP: lateral interparietal area

These studies share a common paradigm: Rhesus macaques view random-dot motion displays. The monkeys' task is to fixate on the stimulus, to determine the direction of net motion, and to indicate the direction of coherent motion by making a saccade in the direction of net motion to one of two targets placed to the right and left of the fixation point. The task is made more or less difficult by changing the percentage of dots with component motion vectors in a particular direction, thus altering the coherence (or strength) of the net motion. By recording from cells in different brain areas during task performance, neuronal contributions to decision can be elucidated.

Cells in visual areas MT (middle temporal) and MST (medial superior temporal) are tuned to motion in particular directions. Recording from cells in these areas whose receptive fields are coincident with the location of the visual stimulus indicates that their neural activity reflects the momentary strength of the motion signal in the cell's preferred direction of motion (Britten et al. 1992, Celebrini & Newsome 1994, Newsome et al. 1989). Neural activity in area LIP (lateral interparietal area) shows a different profile. Neurons in LIP represent both visual and motor information (Shadlen & Newsome 1996). LIP cells appear to integrate signals from extrastriate motion areas over time (Huk & Shadlen 2005); they are also active in the planning and execution of eye movements (Andersen & Buneo 2002).

In the random-dot motion task, for example, a stimulus with a strong coherent motion signal to the right will lead to a ramping up of activity in LIP neurons whose response field encompasses the corresponding saccade target (Shadlen & Newsome 2001). The rate of increase in firing is proportional to motion strength, and when the activity in the LIP neurons reaches a certain absolute level, the monkey makes a saccade to the target, and firing ceases (Roitman & Shadlen 2002). Thus, LIP neurons seem to accumulate evidence of motion strength from sensory areas, until a certain threshold is reached, and a decision is made (Huk & Shadlen 2005). This interpretation is strengthened by the finding that if the monkey is trained to withhold its response until cued, LIP neurons with response fields in the planned response direction maintain elevated firing rates during the delay period, and only cease their activity after the saccade. Thus, unlike neurons in MT and MST, these neurons are not purely stimulus driven, and their continued firing in the absence of the stimulus is taken to reflect the maintenance of the monkey's "decision" about the motion direction of the stimulus, until the completion of the task (Shadlen & Newsome 2001). Activity in these neurons predicts the monkey's response, in both correct and incorrect trials (Shadlen & Newsome 2001). Other experiments provide evidence for the causal involvement of LIP neurons in the decision-making process. For example, microstimulation of LIP neurons with response fields corresponding to a saccade target biases the monkey's choice and affect the timing of its responses (Hanks et al. 2006).

These neural processes have been mathematically modeled and incorporated in race-to-threshold or accumulate-to-bound mathematical models that capture well the behavioral patterns exhibited by the monkeys (Gold & Shadlen 2007, Mazurek et al. 2003). Psychophysical studies in humans indicate that monkeys and humans perform this task similarly, suggesting that analogous neuronal processes are involved in our decisions about these motion stimuli (Palmer et al. 2005).

One may, however, question whether the task of making a decision based on motion stimuli has much do to with the sorts of decisions we typically care about, especially when thinking of decision-making as a manifestation of volition. After all, one might argue (*a*) that the sorts of decisions to which moral responsibility applies, and for which the notion of voluntariness is important, involve much more complex considerations of value, consequences, reasons, feelings, and so on, than this simple perceptual system does; and (*b*) that the stimulus-driven nature of this task is precisely what we do not mean by volition, which is by definition endogenous. This paradigm seems too impoverished to serve as a model for voluntary choice in the light of these considerations.

There are ways of conceiving of these studies in a more general way, making it easier to imagine how this model could serve as the core of a model of human decision-making. In these monkey studies, populations of neurons with particular response properties represent the choices the monkey can make in the task, and their relative firing rates appear to represent the weight given to them during the process leading to decision. We might conceive of these neuronal populations as representing distinct hypotheses or alternatives, such as "motion to the right/left," or alternatively "move eyes to the right/left target." If this is accurate, these neurons are part of representations with propositional content corresponding to the decision alternatives (Gold & Shadlen 2007). It is not difficult to imagine that different neural populations can represent other propositions, and although we currently lack a general framework for conceiving of how propositional content is represented in the nervous system, we know that it can be because we do represent it. Once we can conceive of the neural representation of abstract propositions, it is but a small step to think of them as representing reasons or considerations for action, and their relative firing rates as reflecting the weight given to reasons for decision or action. When we think of free actions, or actions for which we are morally responsible, those actions typically are—or are based on—our decisions in response to reasons (Fischer & Ravizza 1998).

What is more, a number of studies have extended this paradigm in novel ways, suggesting how the general paradigm can incorporate the richer, more nuanced, and abstract considerations that bear on human decision-making. For example, the firing rates of neurons in LIP that are associated with decisions in the visual motion task are also influenced by the expected value of the outcome and its probability, and these play a role in the decision-calculus (Platt & Glimcher 1999, Yang & Shadlen 2007). So outcomes (decisions) associated with higher reward are more heavily weighted, and the time course of the rise to threshold occurs more rapidly to outcomes with higher payoff or those the animal has come to expect as more likely to occur. The firing of these neurons seems to encode the many aspects of decision-making recognized by classical decision theory and embodied in the concept of subjective value (Dorris & Glimcher 2004, Glimcher 2001, Platt & Glimcher 1999). Similar computations occur when the number of options is increased, suggesting that this sort of model can be generalized to decisions with multiple outcomes (Churchland et al. 2008). This system thus provides a basic framework for conceptualizing the main elements central to human decision-making of the most subtle and nuanced sorts.

In most trials, the random-dot motion task is perceptually driven: The nature of the stimulus itself specifies the correct choice. However, the decisions are usually made in conditions of uncertainty, and in some trials the stimulus does not provide determinative evidence for the decision. Monkeys are occasionally presented with random dot motion displays that have 0% coherent motion. Although there is a visual stimulus, the information in the stimulus is ambiguous and unrelated to a "correct" or rewarded choice. Still, in these trials monkeys choose rightward and leftward directions seemingly randomly, even in response to identical movies of 0% motion. The monkey's choices thus are not driven entirely by the external stimulus, but rather by factors internal to the monkey himself. And although the activity levels of the populations representing the alternative choices are nearly evenly matched, slight correlations are found between small fluctuations in activity in LIP in one direction or another, and the monkey's ultimate response (Britten et al. 1996, Shadlen et al. 1996). This suggests that the responses are indeed driven by competition between these neuronal populations.

Some might take the existence of the correlation between neural firing levels and choice even in these 0% motion cases to be evidence for determinism, whereas others could view the

Libertarian freedom: a view that we have free will in virtue of the falsity of determinism

stimulus-independent fluctuations as evidence for the existence and efficacy of random noise in decision-making. I think neither position is warranted, for reasons specified earlier. One person's noise is another person's signal, and without being able to record from all the neural inputs to a system, one cannot determine whether such activity is truly due to stochastic variability of neuronal firing, or is activity due to inputs from other parts of a dynamically evolving system, from local ongoing activity, or is from nonstimulus-related environmental inputs. Without being able to rule out these alternatives, we cannot ascertain whether these fluctuations are due to indeterministic processes or not, and whether the inputs should be viewed as noise or just unidentified signal. For these reasons, given our current knowledge, it seems insufficient to point to them as a basis for libertarian freedom or for the absence thereof.

Although the work on the neural basis of decision-making does not help adjudicate between traditional questions of freedom, if taken to be a general model for the neural basis of decision-making, it is illuminating. This work provides a relatively comprehensive model of a decision process in that it incorporates all the basic elements we would intuitively expect—representation of options, value, evidence, a dynamical characterization of the evolution of the system over time with changing inputs, and even confidence (Kiani & Shadlen 2009). It is only the first pass at a characterization, and there are relevant differences with human decision-making. For example, this system is tightly circumscribed by the task the animal has been trained to do, and the neural bases for decision and motor preparation are intimately related (Gold & Shadlen 2000). If the same stimulus is used but the response indicating the decision is not oculomotor, evidence suggests that other neuronal populations, not in LIP, will represent the decision of direction of motion (Cui & Andersen 2007, Gold & Shadlen 2007). In contrast, some human decision-making may operate at a more abstract level—certainly humans can make decisions in the absence of responses that necessitate concrete motor representations. Whether monkeys can also make abstract decisions remains an open question. Moreover, the picture we currently have is still only a partial and piecemeal view of what the brain is doing during any decision process. Many other brain areas also contribute to decision-making. For example, neuronal activity in DLPFC was also predictive of the monkey's decision in the random-dot motion task (Kim & Shadlen 1999), and responses were sensitive to expected reward value (Leon & Shadlen 1999). This region of monkey cortex is reciprocally connected with the parietal regions discussed above, and temporal coordination of these regions could be important in decision-making (Pesaran et al. 2008). Other areas involved in reward processing are also undoubtedly involved (see O'Doherty 2001, Schultz et al. 2000).

How does the work on decision relate to work on intention? In the random dot motion paradigm discussed above, it is tempting to identify the neural activity in LIP with intention: that activity seems to be causally linked to the production of a response, and when the monkey is required to delay its response, activity in LIP persists in the absence of the stimulus, exactly what one would expect of an intention that bridges the temporal gap between deliberation and action. However, as noted, activity in LIP is modality specific, reflecting a particular motor intention, one that involves eye movements, and not an amodal response. It is possible that most intentions, even many intentions of human animals, are realized in modality-specific motor programs. However, it is also possible that there are amodal means of representing intentions for future action for which there is no clear motor response, such as the intention to finish college, to search for a job, etc. There is some evidence in humans linking DLPFC to decisions independent of response modality (Heekeren et al. 2008). Language may make possible such representations in humans. Depending upon how linguistic abilities arise from neural computation, monkey neurophysiology may or may not provide insight into the nature of linguistically encoded intention.

Despite some shortcomings as a model of human decision-making, the monkey work on decision encourages us to think about volition mechanistically. Some philosophers argue that it is not determinism, but the recognition that mechanism underlies our decisions, that is the most potent challenge to freedom (Nahmias et al. 2007). Although there is some evidence to support this notion, there is much we do not understand about the threat of mechanism, and the relation of mechanism to reductionism. If mechanism is inimical to freedom, it may well be that our growing understanding of mechanisms underlying decision-making will undermine our conception of the will as free, but it is equally conceivable that our views about freedom will adapt to embrace the insights this research provides into the processes underlying our ability to choose among options when the correct choice is not externally dictated.

Volition as Executive Control

The control aspect of volition is the notion that higher-order cortical regions can influence the execution of action by lower regions. This may take several forms. For example, one conception is that volition involves the conscious selection of action (Bunge 2004, Donohue et al. 2008, Fleming et al. 2009, Hyder et al. 1997, Lau et al. 2004b, Matsumoto et al. 2003, Rowe et al. 2008, Rushworth 2008). Another is that monitoring can affect the form an action takes as it is executed (Barch et al. 2000, Kerns et al. 2004, Ridderinkhof et al. 2004, Schall & Boucher 2007, Schall et al. 2002). It is but a step further to think of control as including a capacity to inhibit an intended or planned action (Aron et al. 2007, Brass & Haggard 2007, Brown et al. 2008, Kühn et al. 2009b). The capacity to control one's behavior by inhibiting inappropriate actions is one that some parts of the law recognize as important for legal culpability.

Frontal cortex is generally implicated in executive control, but frontal cortex is a large and heterogeneous area, and much remains to be determined about the functional role of frontal subregions. Some regions of frontal cortex appear to be of particular importance to executive control. Numerous studies implicate interactions between PFC and regions of parietal cortex in attentional control and task switching (Badre 2008; Bode & Haynes 2009; Chiu & Yantis 2009; Dosenbach et al. 2007, 2008; Praamstra et al. 2005; Rossi et al. 2009; Serences & Yantis 2007). Other regions of cortex, such as some parietal regions, seem to play a role in guiding action that is under way (Dosenbach et al. 2007, 2008).

Several regions in frontal cortex appear time and time again in studies on volition. DLPFC is activated in many tasks involving choice or decision-making (Cunnington et al. 2006, Heekeren et al. 2006, Jahanshahi et al. 1995, Kim & Shadlen 1999, Lau et al. 2004a). DLPFC has been implicated in abstract and concrete decisions, as it is activated in choices between actions and in rule selection (Assad et al. 1998; Bunge 2004; Bunge et al. 2003, 2005; Donohue et al. 2008; Rowe et al. 2008). As noted earlier, there are competing hypotheses about the role of DLPFC in tasks involving choice and selection of action, including response selection, conscious deliberation, and conflict resolution. Although some work suggests that DLPFC activity is reflective of attention to selection of action (and thus, presumably, conscious control) (Lau et al. 2004b), other studies indicate that DLPFC activation is not always to be associated with conscious pathways (Lau & Passingham 2007). DLPFC has also been implicated in more abstract forms of control in humans. For example, Knoch & Fehr's (2007) rTMS studies indicate that the capacity to resist temptation depends on right DLPFC.

Discerning the networks subserving voluntary inhibitory control of action appears to be more straightforward. Libet, who argued on the basis of his experimental evidence that conscious intention is not causally efficacious in producing action, consoled himself with the view that the lag between the RP and action could possibly allow for inhibition of unconsciously generated actions, thus preserving the spirit of free will with "free won't" (Libet et al. 1983b) (**Figure 1**). However, he left this as pure conjecture. More recent studies have begun to shed light upon the neural mechanisms of inhibition of intended actions (although they lack the dualistic flavor Libet may have expected for "free won't" to really be free). For example, Brass & Haggard (2007) recently performed fMRI experiments in which they report increased activity in frontomedial cortical areas in Libet-like tasks in which subjects are required to intend to respond, and then to choose randomly to inhibit that response. They conjecture that these frontomedial areas are involved in voluntarily inhibiting self-generated action. Similar regions are involved in decisions to inhibit prepotent responses (Kühn et al. 2009b). Connectivity analyses suggest that medial frontal inhibition influences preSMA in a top-down fashion (Kühn et al. 2009b). Other evidence suggests that inhibition occurs at lower levels in the motor hierarchy as well, for example in local cortical networks in primary motor areas (Coxon et al. 2006).

Whereas dorsal medial frontal regions appear to be involved directly in inhibitory processes, the same regions that mediate voluntary decisions to act appear to be involved in voluntary decisions to refrain from action. Evidence from both ERP and fMRI studies demonstrate that the neural signatures of intentionally not acting, or deciding not to act after forming an intention to act, look very much like those of decisions to act (Kühn & Brass 2009b, Kühn et al. 2009a). For example, areas in anterior cingulate cortex and dorsal preSMA are active in both freely chosen button presses and free decisions not to press a button. The similar neural basis between decisions to act and to refrain from action lends credence to the commonsensical notion that both actions and omissions are acts of the will for which we can be held responsible.

Volition as a Feeling

The experience of willing is an aspect of a multifaceted volitional capacity. Some think that experience is all there is to explain because it is an experience of an otherwise illusory will (Wegner 2002). There are at least two phenomenological aspects of agency: the awareness of an intention or urge to act that we identify as prior to the action, and the post hoc feeling that an action taken was one's own.

With respect to the first, recent results reveal that the experience of voluntary intention depends upon parietal cortex (**Figure 2**). Electrical stimulation in this area elicited motor intentions, and stronger stimulation sometimes led to the erroneous belief that movement had occurred (Desmurget et al. 1999). In contrast, stimulation of premotor cortex led to movements without awareness of movement (Desmurget et al. 2009). Although this suggests that awareness of agency relies primarily on parietal rather than premotor areas, Fried et al. reported that stimulation in SMA also evoked desires to move. Intentions triggered by stimulation in SMA, in contrast to those triggered by parietal stimulation, had the phenomenology of compulsions more than of voluntary intentions (Fried et al. 1991). Although Desmurget et al. did not find that prefrontal stimulation elicited felt intention, the sites in BA6 that they stimulated tended to be more lateral than the regions stimulated by Fried et al. In addition, lesions in the inferior parietal lobe alter the awareness of timing of motor intention. Instead of becoming aware of intentions prior to movement, these lesion patients reported awareness only immediately prior to the time of movement (Sirigu et al. 2004). In contrast, their ability to report movement timing accurately was not impaired.

Considerable progress is also being made in identifying the neural signals involved in production of the feeling of agency or ownership of action (**Figure 2**). The feeling of agency seems to depend upon both proprioceptive and perceptual feedback from the effects of the action (Kühn & Brass 2009a, Moore & Haggard 2008, Moore et al. 2009, Pacherie 2008, Tsakiris et al. 2005). A number of studies indicate that plans for action are often accompanied by efferent signals that allow the system to form expectations for further sensory feedback, which, if not violated, contribute to the feeling of agency (Linser & Goschke 2007, Sirigu et al. 2004). Grafton and colleagues found activation in right angular gyrus (inferior parietal cortex) in cases of discrepancy between anticipated and actual movement outcome, and in awareness of authorship (Farrer et al. 2008). Signals from parietal cortex when predictions of a forward model match sensory or proprioceptive information may be important in creating the sense of agency. Moreover, some aspects of awareness of agency seem constructed retrospectively. A recent study shows that people's judgments about the time of formation of intention to move can be altered by time-shifting sensory feedback, leading to the suggestion that awareness of intention is inferred at least in part from responses, rather than directly perceived (Banks & Isham 2009). Expectation can also play a role (Voss et al. 2008). These studies lend credence to criticisms that the Libet measurement paradigm may affect the reported time of awareness of intention (Lau et al. 2006, 2007). In addition, perceived onset of action relative to effects is modulated by whether the actor perceives the action as volitional (Engbert et al. 2008, Haggard 2008).

As noted, frontal regions may also contribute to awareness of intention. Fried's stimulation study showed that stimulation of regions of SMA (probably pre-SMA) can lead to awareness of intention (Fried et al. 1991). TMS over SMA after action execution also affects the reported time of awareness of intention (Lau et al. 2007), further evidence that awareness of intention is in part reconstruction.

These results are consistent with a model in which parietal cortex generates motor intentions and a predictive signal or forward model for behavior during voluntary action (**Figure 2**). The motor plans are relayed to frontal regions for execution, and activation of these regions may be crucial for aspects of awareness of intention and timing. At the same time, parietal regions compare the internal predictions with sensory feedback [although a recent promising model suggests that the comparator resides in premotor cortex (Desmurget & Sirigu 2009)]. Feedback signals alone are insufficient for a sense of authorship (Tsakiris et al. 2005). When signals match, we may remain unaware of our motor intentions (Sirigu et al. 2004), yet perceive the actions as our own. We may only be made aware of our motor intentions when discrepancies between the forward model and information from perception are detected. Thus, both an efferent internal model and feedback from the environment is important in the perception of agency and self-authorship (Moore et al. 2009).

Under normal circumstances, we experience our voluntary actions as voluntary. Under abnormal circumstances, people may wrongly attribute, or fail to attribute, agency to themselves (Wegner 2002, Wegner & Wheatley 1999). That feelings of agency have led some to suggest that it is merely an illusion that the will is causally efficacious (Hallett 2007, Wegner 2002). However, although experience of agency is not always veridical, we should not conclude that, in general, feelings of agency do not reflect actual agency, that the will is not causally efficacious, or that free will is nothing more than a feeling. The mere fact that the experience of volition has neural underpinnings is also not a basis for denying freedom of the will. Understanding better the interactions between circuits mediating the experience of agency and those involved in initiation of movement, formation of intention, etc., may explain how these various aspects of volition are related and can be dissociated, both with particular forms of brain damage, or with given certain arrangements of external events.

CONCLUDING THOUGHTS

On the whole, neuroscience has not much affected our conception of volition. It has maintained in large part notions of intention, choice, and the experience of agency. Where neuroscience has affected our conception, it has typically challenged traditional views of the relationship between consciousness and action. For example, more aspects of behavior than previously imagined are governed by unconscious processes. However, since we have little traction on the neural basis of consciousness, none of those challenges, to my mind, has succeeded in undermining traditional views. However, neuroscience promises to show volition not to be a unitary faculty, but rather a collection of largely separable processes that together make possible flexible, intelligent action. It may affect our notion of volition in the future by elucidating the neural systems and computations underlying these different aspects of volition. Further elucidation of brain networks may provide a better way of taxonomizing the elements of volition (Brass & Haggard 2008; Pacherie 2006, 2008). Although I believe that neuroscience will not bear upon the question of freedom via a frontal assault on the determinism question, increasing our understanding of the neural bases of these processes might cause us to think of volition more mechanistically than we currently do, and that may ultimately put pressure on our ordinary notions of what is required for freedom. For now, however, the most significant contribution neuroscience has made has been in allowing us to formulate novel questions about the nature of voluntary behavior, and in providing new ways of addressing them.

SUMMARY POINTS

1. What we think of as volition may not be a unitary faculty.
2. Neuroscience will not settle the question of determinism.
3. A network of frontal and parietal regions is involved in initiating, selecting, and controlling voluntary actions.
4. PreSMA and rCZ are implicated in endogenously generated movement.
5. The neural bases of many aspects of decision-making are well understood and can be mathematically modeled.
6. Choices to act and to refrain from acting seem to involve similar brain circuitry.
7. The feeling of agency is mediated in part by parietal cortex; it depends upon both predictive signals and postdictive feedback.
8. Thus far, neither the timing of conscious intention, mechanism, nor illusions of agency undermine the existence or efficacy of the will.

FUTURE ISSUES

1. What is the challenge that mechanism poses for accounts of volition and freedom?
2. How do different circuits mediating choice, planning, action initiation, control, and feelings of agency interact with each other?
3. How do those circuits involve, underlie, and interact with representations of self?
4. What neural computations underlie the signals identified in voluntary action in the preSMA and rCZ, and what roles do they play in action initiation?
5. What processes set the threshold and/or baseline activity in decision-making?
6. How do internal loops make possible action that is not stimulus-bound?

7. How do frontal areas control, regulate, and modify neural activity in other brain areas?
8. What are the sources of variability in the nervous system? What role does noise play in choice and action?

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This work was supported in part by an NEH collaborative research grant to the Johns Hopkins Berman Institute of Bioethics, and by the MacArthur Project in Law and Neuroscience. I would like to thank Eran Klein, Nancy McConnell, Al Mele, Shaun Nichols, Michael Shadlen, and Walter Sinnott-Armstrong for comments on an earlier draft.

LITERATURE CITED

Adams F, Mele A. 1992. The intention/volition debate. *Can. J. Philos.* 22:323–38

Andersen RA, Buneo CA. 2002. Intentional maps in posterior parietal cortex. *Annu. Rev. Neurosci.* 25:189–220

Andersen RA, Buneo CA. 2003. Sensorimotor integration in posterior parietal cortex. *Adv. Neurol.* 93:159–77

Aron AR, Behrens TE, Smith S, Frank MJ, Poldrack RA. 2007. Triangulating a cognitive control network using diffusion-weighted magnetic resonance imaging (MRI) and functional MRI. *J. Neurosci.* 27:3743–52

Assad WF, Rainer G, Miller EK. 1998. Neural activity in the primate prefrontal cortex during associative learning. *Neuron* 21:1399–407

Audi R. 1993. Volition and agency. In *Action, Intention, and Reason*, ed. AR Mele, pp. 74–108. Ithaca, NY: Cornell Univ. Press

Badre D. 2008. Cognitive control, hierarchy, and the rostro-caudal organization of the frontal lobes. *Trends Cogn. Sci.* 12:193–200

Banks WP, ed. 2002. *Consciousness and Cognition*, Vol. 11. New York: Academic Press

Banks WP, Isham EA. 2009. We infer rather than perceive the moment we decided to act. *Psychol. Sci.* 20:17–21

Banks WP, Pockett S. 2007. Benjamin Libet's work on the neuroscience of free will. In *Blackwell Companion to Consciousness*, ed. M Velmans, S Schinder, pp. 657–70. Malden, MA: Blackwell

Barch DM, Braver TS, Sabb FW, Noll DC. 2000. Anterior cingulate and the monitoring of response conflict: evidence from an fMRI study of overt verb generation. *J. Cogn. Neurosci.* 12:298–309

Bittner T. 1996. Consciousness and the act of will. *Philos. Stud.* 81:331–41

Bode S, Haynes JD. 2009. Decoding sequential stages of task preparation in the human brain. *NeuroImage* 45:606–13

Brass M, Haggard P. 2007. To do or not to do: the neural signature of self-control. *J. Neurosci.* 27:9141–45

Brass M, Haggard P. 2008. The what, when, whether model of intentional action. *Neuroscientist* 14:319–25

Britten KH, Newsome WT, Shadlen MN, Celebrini S, Movshon JA. 1996. A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Vis. Neurosci.* 13:87–100

Britten KH, Shadlen MN, Newsome WT, Movshon JA. 1992. The analysis of visual motion: a comparison of neuronal and psychophysical performance. *J. Neurosci.* 12:4745–65

Brown JW, Hanes DP, Schall JD, Stuphorn V. 2008. Relation of frontal eye field activity to saccade initiation during a countermanding task. *Exp. Brain Res.* 190:135–51

Bunge SA. 2004. How we use rules to select actions: a review of evidence from cognitive neuroscience. *Cogn. Affect. Behav. Neurosci.* 4:564–79

Bunge SA, Kahn I, Wallis JD, Miller EK, Wagner AD. 2003. Neural circuits subserving the retrieval and maintenance of abstract rules. *J. Neurophysiol.* 90:3419–28

Bunge SA, Wallis JD, Parker A, Brass M, Crone EA, et al. 2005. Neural circuitry underlying rule use in humans and nonhuman primates. *J. Neurosci.* 25:10347–50

Celebrini S, Newsome WT. 1994. Neuronal and psychophysical sensitivity to motion signals in extrastriate area MST of the macaque monkey. *J. Neurosci.* 14:4109–24

Chiu Y-C, Yantis S. 2009. A domain-independent source of cognitive control for task sets: shifting spatial attention and switching categorization rules. *J. Neurosci.* 29:3930–38

Churchland AK, Kiani R, Shadlen MN. 2008. Decision-making with multiple alternatives. *Nat. Neurosci.* 11:693–702

Ciaramidaro A, Adenzato M, Enrici I, Erk S, Pia L, et al. 2007. The intentional network: how the brain reads varieties of intentions. *Neuropsychologia* 45:3105–13

Corbetta M, Miezin FM, Dobmeyer S, Shulman GL, Petersen SE. 1990. Attentional modulation of neural processing of shape, color, and velocity in humans. *Science* 248:1556–59

Coxon JP, Stinear CM, Byblow WD. 2006. Intracortical inhibition during volitional inhibition of prepared action. *J. Neurophysiol.* 95:3371–83

Cui H, Andersen RA. 2007. Posterior parietal cortex encodes autonomously selected motor plans. *Neuron* 56:552–59

Cunnington R, Windischberger C, Deecke L, Moser E. 2002. The preparation and execution of self-initiated and externally-triggered movement: a study of event-related fMRI. *NeuroImage* 15:373–85

Cunnington R, Windischberger C, Robinson S, Moser E. 2006. The selection of intended actions and the observation of others' actions: a time-resolved fMRI study. *NeuroImage* 29:1294–302

Deecke L, Kornhuber HH. 1978. An electrical sign of participation of the mesial 'supplementary' motor cortex in human voluntary finger movement. *Brain Res.* 159:473–76

Deiber M-P, Honda M, Ibanez V, Sadato N, Hallett M. 1999. Mesial motor areas in self-initiated versus externally triggered movements examined with fMRI: effect of movement type and rate. *J. Neurophysiol.* 81:3065–77

de Lange FP, Spronk M, Willems RM, Toni I, Bekkering H. 2008. Complementary systems for understanding action intentions. *Curr. Biol.* 18:454–57

den Ouden HE, Frith U, Frith C, Blakemore SJ. 2005. Thinking about intentions. *NeuroImage* 28:787–96

Desmurget M, Epstein CM, Turner RS, Prablanc C, Alexander GE, Grafton ST. 1999. Role of the posterior parietal cortex in updating movements to a visual target. *Nat. Neurosci.* 2:563–67

Desmurget M, Reilly KT, Richard N, Szathmari A, Mottolese C, Sirigu A. 2009. Movement intention after parietal cortex stimulation in humans. *Science* 324:811–13

Desmurget M, Sirigu A. 2009. A parietal-premotor network for movement intention and motor awareness. *Trends Cogn. Sci.* 13:411–19

Donohue SE, Wendelken C, Bunge SA. 2008. Neural correlates of preparation for action selection as a function of specific task demands. *J. Cogn. Neurosci.* 20:694–706

Dorris MC, Glimcher PW. 2004. Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. *Neuron* 44:365–78

Dorval AD. 2006. The rhythmic consequences of ion channel stochasticity. *Neuroscientist* 12:442–48

Dosenbach NUF, Fair DA, Cohen AL, Schlaggar BL, Petersen SE. 2008. A dual-networks architecture of top-down control. *Trends Cogn. Sci.* 12:99–105

Dosenbach NUF, Fair DA, Miezin FM, Cohen AL, Wenger KK, et al. 2007. Distinct brain networks for adaptive and stable task control in humans. *Proc. Natl. Acad. Sci. USA* 104:11073–78

Engbert K, Wohlschlager A, Haggard P. 2008. Who is causing what? The sense of agency is relational and efferent-triggered. *Cognition* 107:693–704

Farrer C, Frey SH, Van Horn JD, Tunik E, Turk D, et al. 2008. The angular gyrus computes action awareness representations. *Cereb. Cortex* 18:254–61

Fischer J, Ravizza M. 1998. *Responsibility and Control: A Theory of Moral Responsibility*. New York: Cambridge Univ. Press

Fleming SM, Mars RB, Gladwin TE, Haggard P. 2009. When the brain changes its mind: flexibility of action selection in instructed and free choices. *Cereb. Cortex* 19:2352–50

Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G. 2005. Parietal lobe: from action organization to intention understanding. *Science* 308:662–67

Franks KM, Stevens CF, Sejnowski TJ. 2003. Independent sources of quantal variability at single glutamatergic synapses. *J. Neurosci.* 23:3186–95

Fried I, Katz A, McCarthy G, Sass K, Williamson P, et al. 1991. Functional organization of human supplementary motor cortex studied by electrical stimulation. *J. Neurosci.* 11:3656–66

Frith CD, Friston K, Liddle PF, Frackowiak RSJ. 1991. Willed action and the prefrontal cortex in man: a study with PET. *Proc. R. Soc. Lond. Ser. B* 244:241–46

Glimcher PW. 2001. Making choices: the neurophysiology of visual-saccadic decision making. *Trends Neurosci.* 24:654–59

Glimcher PW. 2003. The neurobiology of visual-saccadic decision making. *Annu. Rev. Neurosci.* 26:133–79

Glimcher PW. 2005. Indeterminacy in brain and behavior. *Annu. Rev. Psychol.* 56:25–56

Gold JI, Shadlen MN. 2000. Representation of a perceptual decision in developing oculomotor commands. *Nature* 404:390–94

Gold JI, Shadlen MN. 2007. The neural basis of decision making. *Annu. Rev. Neurosci.* 30:535–74

Haggard P. 2005. Conscious intention and motor cognition. *Trends Cogn. Sci.* 9:290–95

Haggard P. 2008. Human volition: towards a neuroscience of will. *Nat. Rev. Neurosci.* 9:934–46

Haggard P, Eimer M. 1999. On the relation between brain potentials and the awareness of voluntary movements. *Exp. Brain Res.* 126:128–33

Hallett M. 2007. Volitional control of movement: the physiology of free will. *Clin. Neurophysiol.* 118:1179–92

Hamilton AF, Grafton ST. 2006. Goal representation in human anterior intraparietal sulcus. *J. Neurosci.* 26:1133–37

Hanks TD, Ditterich J, Shadlen MN. 2006. Microstimulation of macaque area LIP affects decision-making in a motion discrimination task. *Nat. Neurosci.* 9:682–89

Haynes JD, Sakai K, Rees G, Gilbert S, Frith C, Passingham RE. 2007. Reading hidden intentions in the human brain. *Curr. Biol.* 17:323–28

Heekeren HR, Marrett S, Ruff DA, Bandettini PA, Ungerleider LG. 2006. Involvement of human left dorsolateral prefrontal cortex in perceptual decision making is independent of response modality. *Proc. Natl. Acad. Sci. USA* 103:10023–28

Heekeren HR, Marrett S, Ungerleider LG. 2008. The neural systems that mediate human perceptual decision making. *Nat. Rev. Neurosci.* 9:467–79

Hesse MD, Thiel CM, Stephan KE, Fink GR. 2006. The left parietal cortex and motor intention: an event-related functional magnetic resonance imaging study. *Neuroscience* 140:1209–21

Huk AC, Shadlen MN. 2005. Neural activity in macaque parietal cortex reflects temporal integration of visual motion signals during perceptual decision making. *J. Neurosci.* 25:10420–36

Hyder F, Phelps EA, Wiggins CJ, Labar KS, Blamire AM, Shulman RG. 1997. "Willed action": a functional MRI study of the human prefrontal cortex during a sensorimotor task. *Proc. Natl. Acad. Sci. USA* 94:6989–94

Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. 2005. Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol.* 3:e79

Jahanshahi M, Jenkins IH, Brown RG, Marsden CD, Passingham RE, Brooks DJ. 1995. Self-initiated versus externally triggered movements: I. An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. *Brain* 118:913–33

Jenkins IH, Jahanshahi M, Jueptner M, Passingham RE, Brooks DJ. 2000. Self-initiated versus externally triggered movements: II. The effect of movement predictability on regional cerebral blood flow. *Brain* 123:1216–28

Kennerley SW, Sakai K, Rushworth MFS. 2004. Organization of action sequences and the role of the Pre-SMA. *J. Neurophysiol.* 91:978–93

Kerns JG, Cohen JD, MacDonald AWI, Cho RY, Stenger VA, Carter CS. 2004. Anterior cingulate conflict monitoring and adjustments in control. *Science* 303:1023–26

Kiani R, Shadlen MN. 2009. Representation of confidence associated with a decision by neurons in the parietal cortex. *Science* 324:759–64

Kim J-N, Shadlen MN. 1999. Neural correlates of a decision in the dorsolateral prefrontal cortex of the macaque. *Nat. Neurosci.* 2:176–85

Knoch D, Fehr E. 2007. Resisting the power of temptations: the right prefrontal cortex and self-control. *Ann. NY Acad. Sci.* 1104:123–34

Kühn S, Brass M. 2009a. Retrospective construction of the judgement of free choice. *Conscious Cogn.* 18:12–21

Kühn S, Brass M. 2009b. When doing nothing is an option: the neural correlates of deciding whether to act or not. *NeuroImage* 46:1187–93

Kühn S, Gevers W, Brass M. 2009a. The neural correlates of intending not to do something. *J. Neurophysiol.* 101:1913–20

Kühn S, Haggard P, Brass M. 2009b. Intentional inhibition: how the "veto-area" exerts control. *Hum. Brain Mapp.* 30:2834–43

Lamm C, Fischer MH, Decety J. 2007. Predicting the actions of others taps into one's own somatosensory representations—a functional MRI study. *Neuropsychologia* 45:2480–91

Lau HC, Passingham RE. 2007. Unconscious activation of the cognitive control system in the human prefrontal cortex. *J. Neurosci.* 27:5805–11

Lau HC, Rogers RD, Haggard P, Passingham RE. 2004a. Attention to intention. *Science* 303:1208–10

Lau HC, Rogers RD, Passingham RE. 2006. On measuring the perceived onsets of spontaneous actions. *J. Neurosci.* 26:7265–71

Lau HC, Rogers RD, Passingham RE. 2007. Manipulating the experienced onset of intention after action execution. *J. Cogn. Neurosci.* 19:81–90

Lau HC, Rogers RD, Ramnani N, Passingham RE. 2004b. Willed action and attention to the selection of action. *NeuroImage* 21:1407–15

Leon MI, Shadlen MN. 1999. Effect of expected reward magnitude on the response of neurons in the dorsolateral prefrontal cortex of the macaque. *Neuron* 24:415–25

Libet B. 1985. Unconscious cerebral initiative and the role of conscious will in voluntary action. *Behav. Brain Sci.* 8:529–66

Libet B, Gleason CA, Wright EW, Pearl DK. 1983a. Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential): the unconscious initation of a freely voluntary act. *Brain* 106:623–42

Libet B, Gleason CA, Wright EW, Pearl DK. 1983b. Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential): the unconscious initation of a freely voluntry act. *Brain* 106:623–42

Libet B, Wright EW Jr, Gleason CA. 1982. Readiness-potentials preceding unrestricted "spontaneous" vs preplanned voluntary acts. *Electroencephalogr. Clin. Neurophysiol.* 54:322–35

Libet B, Wright EW Jr, Gleason CA. 1983c. Preparation or intention-to-act, in relation to pre-event potentials recorded at the vertex. *Electroencephalogr. Clin. Neurophysiol.* 56:367–72

Linser K, Goschke T. 2007. Unconscious modulation of the conscious experience of voluntary control. *Cognition* 104:459–75

Mainen ZF, Sejnowski TJ. 1995. Reliability of spike timing in neocortical neurons. *Science* 268:1503–6

Matsuhashi M, Hallett M. 2008. The timing of the conscious intention to move. *Eur. J. Neurosci.* 28:2344–51

Matsumoto K, Suzuki W, Tanaka K. 2003. Neuronal correlates of goal-based motor selection in the prefrontal cortex. *Science* 301:229–32

Mazurek ME, Roitman JD, Ditterich J, Shadlen MN. 2003. A role for neural integrators in perceptual decision making. *Cereb. Cortex* 13:1257–69

Mele AR. 2006. *Free Will and Luck*. Oxford: Oxford Univ. Press

Mele AR. 2009. *Effective Intentions: The Power of Conscious Will*. New York: Oxford Univ. Press

Monterosso J, Royzman EB, Schwartz B. 2005. Explaining away responsibility: effects of scientific explanation on perceived culpability. *Ethn. Behav.* 15:139–58

Moore J, Haggard P. 2008. Awareness of action: Inference and prediction. *Conscious Cogn.* 17:136–44

Moore JW, Lagnado D, Deal DC, Haggard P. 2009. Feelings of control: Contingency determines experience of action. *Cognition* 110:279–83

Mueller VA, Brass M, Waszak F, Prinz W. 2007. The role of the preSMA and the rostral cingulate zone in internally selected actions. *NeuroImage* 37:1354–61

Nachev P, Kennard C, Husain M. 2008. Functional role of the supplementary and presupplementary motor areas. *Nat. Rev. Neurosci.* 9:856–69

Nachev P, Rees G, Parton A, Kennard C, Husain M. 2005. Volition and conflict in human medial frontal cortex. *Curr. Biol.* 15:122–28

Nahmias E, Coates DJ, Kvaran T. 2007. Free will, moral responsibility, and mechanism: experiments on folk intuitions. *Midwest Stud. Philos.* 31:215–42

Newsome WT, Britten KH, Movshon JA. 1989. Neuronal correlates of a perceptual decision. *Nature* 341:52–54

O'Craven KM, Rosen BR, Kwong KK, Treisman AM, Savoy RL. 1997. Voluntary attention modulates fMRI activity in human MT-MST. *Neuron* 18:591–98

O'Doherty JEA. 2001. Abstract reward and punishment representations in the human orbitofrontal cortex. *Nat. Neurosci.* 4:95–102

Pacherie E. 2006. Toward a dynamic theory of intentions. In *Does Consciousness Cause Behavior? An Investigation of the Nature of Volition*, ed. S Pockett, WP Banks, S Gallagher, pp. 145–67. Cambridge, MA: MIT Press

Pacherie E. 2008. The phenomenology of action: a conceptual framework. *Cognition* 107:179–217

Palmer J, Huk AC, Shadlen MN. 2005. The effect of stimulus strength on the speed and accuracy of a perceptual decision. *J. Vis.* 5:376–404

Pesaran B, Nelson MJ, Andersen RA. 2008. Free choice activates a decision circuit between frontal and parietal cortex. *Nature* 453:406–9

Picard N, Strick PL. 1996. Motor areas of the medial wall: a review of their location and functional activation. *Cereb. Cortex* 6:342–53

Picard N, Strick PL. 2001. Imaging the premotor areas. *Curr. Opin. Neurobiol.* 11:663–72

Platt ML, Glimcher PW. 1999. Neural correlates of decision variables in parietal cortex. *Nature* 400:233–38

Praamstra P, Boutsen L, Humphreys GW. 2005. Frontoparietal control of spatial attention and motor intention in human EEG. *J. Neurophysiol.* 94:764–74

Quian Quiroga R, Snyder LH, Batista AP, Cui H, Andersen RA. 2006. Movement intention is better predicted than attention in the posterior parietal cortex. *J. Neurosci.* 26:3615–20

Ramnani N, Miall RC. 2004. A system in the human brain for predicting the actions of others. *Nat. Neurosci.* 7:85–90

Ridderinkhof KR, Ullsperger M, Crone EA, Nieuwenhuis S. 2004. The role of the medial frontal cortex in cognitive control. *Science* 306:443–47

Rizzolatti G, Sinigaglia C. 2007. Mirror neurons and motor intentionality. *Funct. Neurol.* 22:205–10

Roitman JD, Shadlen MN. 2002. Response of neurons in the lateral intraparietal area during a combined visual discrimination reaction time task. *J. Neurosci.* 22:9475–89

Roskies AL. 2006. Neuroscientific challenges to free will and responsibility. *Trends Cogn. Sci.* 10:419–23

Roskies AL. 2010. Why Libet's studies don't pose a threat to free will. In *Conscious Will and Responsibility*, ed. W Sinnott-Armstrong, L Nadel. New York: Oxford Univ. Press. In press

Rossi AF, Pessoa L, Desimone R, Ungerleider LG. 2009. The prefrontal cortex and the executive control of attention. *Exp. Brain Res.* 192:489–97

Rowe J, Hughes L, Eckstein D, Owen AM. 2008. Rule-selection and action-selection have a shared neuroanatomical basis in the human prefrontal and parietal cortex. *Cereb. Cortex* 18:2275–85

Rushworth MF. 2008. Intention, choice, and the medial frontal cortex. *Ann. NY Acad. Sci.* 1124:181–207

Schall JD, Boucher L. 2007. Executive control of gaze by the frontal lobes. *Cogn. Affect. Behav. Neurosci.* 7:396–412

Schall JD, Stuphorn V, Brown JW. 2002. Monitoring and control of action by the frontal lobes. *Neuron* 36:309–22

Schultz W, Tremblya L, Hollerman JR. 2000. Reward processing in primate orbitofrontal cortex and basal ganglia. *Cereb. Cortex* 10:272–83

Searle JR. 1983. *Intentionality: An Essay in the Philosophy of Mind.* Cambridge, UK: Cambridge Univ. Press

Serences JT, Yantis S. 2007. Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. *Cereb. Cortex* 17:284–93

Shadlen MN, Britten KH, Newsome WT, Movshon JA. 1996. A computational analysis of the relationship between neuronal and behavioral responses to visual motion. *J. Neurosci.* 16:1486–510

Shadlen MN, Newsome WT. 1996. Motion perception: seeing and deciding. *Proc. Natl. Acad. Sci. USA* 93:628–33

Shadlen MN, Newsome WT. 2001. Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. *J. Neurophysiol.* 86:1916–36

Shibasaki H, Hallett M. 2006. What is the Bereitschaftspotential? *Clin. Neurophysiol.* 117:2341–56

Sinnott-Armstrong W, Nadel L, eds. 2010. *Conscious Will and Responsibility*. New York: Oxford Univ. Press. In press

Sirigu A, Daprati E, Ciancia S, Giraux P, Nighoghossian N, et al. 2004. Altered awareness of voluntary action after damage to the parietal cortex. *Nat. Neurosci.* 7:80–84

Soon CS, Brass M, Heinze H-J, Haynes J-D. 2008. Unconscious determinants of free decisions in the human brain. *Nat. Neurosci.* 11:543–45

Sumner P, Nachev P, Morris P, Peters AM, Jackson SR, et al. 2007. Human medial frontal cortex mediates unconscious inhibition of voluntary action. *Neuron* 54:697–711

Thaler D, Chen YC, Nixon PD, Stern CE, Passingham RE. 1995. The functions of the medial premotor cortex. I. Simple learned movements. *Exp. Brain Res.* 102:445–60

Thoenissen D, Zilles K, Toni I. 2002. Differential involvement of parietal and precentral regions in movement preparation and motor intention. *J. Neurosci.* 22:9024–34

Trevena JA, Miller J. 2002. Cortical movement preparation before and after a conscious decision to move. *Conscious Cogn.* 11:162–90

Tsakiris M, Haggard P, Franck N, Mainy N, Sirigu A. 2005. A specific role for efferent information in self-recognition. *Cognition* 96:215–31

Voss M, Ingram JN, Wolpert DM, Haggard P. 2008. Mere expectation to move causes attenuation of sensory signals. *PloS ONE* 3:e2866

Wegner D. 2002. *The Illusion of Conscious Will*. Cambridge, MA: MIT Press

Wegner D, Wheatley T. 1999. Apparent mental causation: sources of the experience of will. *Am. Psychol.* 54:480–92

Yang T, Shadlen MN. 2007. Probabilistic reasoning by neurons. *Nature* 447:1075–80

Young G. 2006. Preserving the role of conscious decision making in the initiation of intentional action. *J. Conscious Stud.* 13:51–68

Zhu J. 2004a. Intention and volition. *Can. J. Philos.* 34:175–93

Zhu J. 2004b. Understanding volition. *Philos. Psychol.* 17:247–73

Annual Review of
Neuroscience

Volume 33, 2010

Contents

Indexes

Errata

An online log of corrections to *Annual Review of Neuroscience* articles may be found at http://neuro.annualreviews.org/