Decision Time for Free Will

Patrick Haggard[1,*]
[1]Institute of Cognitive Neuroscience, University College London, London WC1N 3AR, UK
*Correspondence: p.haggard@ucl.ac.uk
DOI 10.1016/j.neuron.2011.01.028

In this issue of *Neuron*, Fried et al. report electrical recordings from single neurons in several areas of the human medial frontal lobe prior to voluntary movement. These data shed important new light on the neuronal mechanisms of human volition and on the hotly debated relation between consciousness and will.

Introduction

Few issues in neuroscience attract such wide interest as the brain basis of "free will." We all have the strong belief that we make choices about what we do and that our conscious decisions initiate our actions, at least on some occasions. At the same time, our actions are clearly the result of a causal chain of neuronal activity in premotor and motor areas of the brain. Neuroscience has few convincing experimental methods to study the brain processes that precede voluntary action. The few published data available often use recording methods such as fMRI that give only crude or indirect pictures of neuronal activity.

To date, the field has been dominated by the "Libet experiment" (Libet et al., 1983). In this experiment, participants are asked to make a simple voluntary action, such as a key press, whenever they feel like it. Brain activity is measured throughout, originally using EEG and more recently using fMRI (Lau et al., 2004). At the same time, they observe a rotating clock hand and are asked to note the position of the clock when they first experience the conscious intention, or "feel the urge," to press the key. This hotly debated marker of volition is referred to as W (judgment of will, following Libet's terminology). EEG activity over frontal motor areas began 1 s or more before movement (the so-called "readiness potential" [Kornhuber and Deecke, 1965]), while W occurred much later, a few hundred ms before movement itself. These findings raise important questions about the brain events that initiate voluntary actions and their relation to consciousness. Although the Libet experiment was published almost 30 years ago, it is still serves as a nexus in the neuroscience of volition.

The paper by Fried, Mukamel, and Kreiman (Fried et al., 2011) offers a genuinely new perspective on volition. The key contribution comes from the nature of the data themselves. In some cases of intractable epilepsy, intracranial electrodes are used for evaluation prior to neurosurgery. When depth electrodes are inserted into the cortical tissue itself, it is then possible to record the firing patterns of single neurons in awake, behaving humans. The potential value of these kinds of data for understanding cognition cannot be underestimated. Fried and colleagues reprised the Libet experiment while recording from electrodes in medial frontal areas in 12 epileptic patients. These areas generate the scalp readiness potentials recorded prior to voluntary movement. Moreover, stimulation of these areas has been reported to generate a feeling of urge to move a particular body part, without necessarily causing actual movement (Fried et al., 1991). Therefore, direct recordings from medial frontal neurons are an important part of the puzzle of the neuroscience of will.

Preconscious Predictions about Conscious Will

First, the single-neuron data provide a reassuring confirmation of previous studies that recorded neural populations. A relatively small subset of medial frontal neurons showed a gradual ramp-like increase in firing rate before movement that recalls both EEG readiness potentials and recordings prior to memory-guided actions in trained monkeys (Shima and Tanji, 2000). The time of conscious intention could be predicted from small subpopulations of these neurons, using an integrate-and-fire model, well before the time that participants reported the

experience of volition. Of course, the time of conscious intention is closely linked to the time of action itself, so it is difficult to separate the relation between medial frontal activity and conscious intention from the relation between medial frontal activity and voluntary action. In fact, these data give the impression that conscious intention is just a subjective corollary of an action being about to occur. Such models agree with previous accounts that voluntary actions begin unconsciously and enter into our conscious experience only when medial frontal activity has reached a given threshold level of activity (Matsuhashi and Hallett, 2008). In this sense, the current work is in broad agreement with a general trend in neuroscience of volition: although we may experience that our conscious decisions and thoughts cause our actions, these experiences are in fact based on readouts of brain activity in a network of brain areas that control voluntary action.

The novelty of this study, however, lies in the fine grain of detail that it gives about the mechanisms of volitional action. This knowledge fills important gaps that are intrinsic to methods used previously: EEG recordings in humans lacked spatial precision, neuroimaging studies lacked fine temporal precision, and single-unit recording studies in animals lacked any conscious dimension. It is worth summarizing some of the specific details in Fried et al.'s data and considering their implications for neuroscience of human volition.

Involvement of Different Medial Frontal Areas in Coding for Volition

These data provide perhaps the first opportunity to compare the contributions of several different medial frontal areas to volition. Here, there are some interesting surprises. For some years, the

classical supplementary motor area, located immediately anterior to the medial part of the primary motor cortex, has been divided into pre-SMA rostrally and SMA proper more caudally. The pre-SMA was considered to be involved primarily in movement planning, while the SMA proper was considered an execution area, since it sends axons to the spinal cord (Picard and Strick, 1996). These arguments lead many researchers to link the pre-SMA both to voluntary action and to the experience of volition itself. Indeed, pre-SMA was activated in an fMRI study of the Libet task (Lau et al., 2004) and was identified as the source of readiness potentials from subdural recordings (Yazawa et al., 2000). However, Fried et al.'s data interestingly show a very different pattern. SMA proper contained relatively more neurons active before W than did the pre-SMA. In contrast, rather few SMA proper neurons were active in the brief interval between W and movement onset relative to the pre-SMA. A quick statistical test on the proportions of each type of unit in the two areas shows a significant difference in the distributions ($\chi^2(1) = 4.13$, $p = 0.042$). Importantly, the difference is in the *opposite* direction from that suggested by neuroimaging and EEG studies. This finding suggests a revision of how we interpret the W judgment. It is clearly wrong to think of W as a prior intention, located at the very earliest moment of decision in an extended action chain. Rather, W seems to mark an intention-in-action, quite closely linked to action execution. The experience of conscious intention may correspond to the point at which the brain transforms a prior plan into a motor act through changes in activity of SMA proper.

Medial Frontal Neurons whose Firing Decreases Prior to Volition

A second striking finding is the prevalence of cells that are clearly associated with voluntary action, but whose firing rate decreases progressively prior to W. Other methods, such as EEG and neuroimaging, presumably register an aggregated signal, reflecting activity of both "increasing" and "decreasing" neurons. Again, there are interesting differences between the areas recorded, with decreasing neurons being more common than increasing

neurons in the rostral anterior cingulate and also in the pre-SMA. The function of decreasing neurons remains unclear. Of course, the increasing/decreasing profiles could reflect a simple additional computational transformation: a single inhibitory interneuron could transform information between one pattern and the other.

At the same time, it is tempting to take decreasing neurons as evidence for an intrinsically inhibitory component of volition. Several classes of evidence suggest that suppression of action and voluntary initiation are profoundly linked in the medial frontal cortex. First, lesions in this region can produce anarchic hand and utilization behavior involving unwanted, compulsive actions in response to environmental stimuli (Boccardi et al., 2002). This suggests that an important normal function of these areas may be to tonically inhibit unwanted actions. Second, a recent neuroimaging study showed increased pre-SMA activation when an external stop signal successfully triggered inhibition of movement (Sharp et al., 2010). Finally, and compellingly, medial frontal areas that produced movement arrest during intracranial stimulation were also identified as the source of readiness potentials during action generation (Yazawa et al., 2000). A recent model of volition identified the decision of whether to act or not as an important component of volition (Brass and Haggard, 2008). Fried et al.'s data suggest one mechanism that might be involved in this decision. Decreasing neurons might withhold actions until they become appropriate through tonic inhibition and then help to trigger voluntary actions by gradually removing this tonic inhibition. Competitive inhibitory interaction between decreasing and increasing neurons could then provide a circuit for resolving whether to act or withhold action. A similar model has already been proposed for decisions between alternative stimulus-driven actions in lateral premotor cortex (Cisek, 2007). Libet thought that "veto decisions" could represent a form of pure mind-brain causation, with consciousness directly intervening to interrupt the buildup of the readiness potential. Competition between populations of medial frontal neurons may provide a simpler explanation, though it still leaves us hunting for potential "deci-

sion" areas that may modulate the competition.

Outstanding Questions for the Neuroscience of Volition

Not surprisingly, several questions remain unanswered. One is the possible contribution to volition of other cortical areas not studied here. Fried et al. highlight recent reports of an experience of urge to move following parietal stimulation (Desmurget et al., 2009). They briefly present one parietal recording from their own data set, which shows an increase in firing rate prior to W very similar to medial frontal neurons. The division of labor between medial frontal and parietal cortex in volition is a topic of current debate. Neuropsychological studies of patients with focal frontal and parietal lesions suggest that both areas are involved in volition (Haggard, 2008). It seems likely that they act as a concerted network: the pre-SMA might generate action plans, and the parietal cortex might monitor their progression to execution. However, we have little insight into the detailed operation of this network. In neurosurgical studies, the sites of stimulation and placement of recording electrodes are, of course, determined by clinical need alone. Therefore, the crucial data required to resolve the debate, such as simultaneous recordings from parietal and frontal electrodes in the same individual, may not be forthcoming.

A second remaining question is the activity of these neurons in the absence of voluntary action. The technique used here, as in other voluntary action experiments, involves "back-averaging" neural activity time-locked to a motor response. This technique suggests that medial frontal cortex activity is a necessary condition for voluntary action. However, we cannot tell if medial frontal activity is sufficient for action. In fact, we know little about neuronal activity in these areas when no voluntary actions occur. The presence of medial frontal or prefrontal BOLD responses when successfully stopping a voluntary action in response to a stop signal (Sharp et al., 2010) or an internal decision (Brass and Haggard, 2008) suggests that neuronal firing may not be sufficient for action. In principle, buildup of activity in areas such as pre-SMA could occur very frequently, but the

firing trajectory could be prevented from continuing toward voluntary action for some unknown reason.

REFERENCES

Boccardi, E., Della Sala, S., Motto, C., and Spinnler, H. (2002). Cortex *38*, 289–308.

Brass, M., and Haggard, P. (2008). Neuroscientist *14*, 319–325.

Cisek, P. (2007). Philos. Trans. R. Soc. Lond. B. Biol. Sci. *362*, 1585–1599.

Desmurget, M., Reilly, K.T., Richard, N., Szathmari, A., Mottolese, C., and Sirigu, A. (2009). Science *324*, 811–813.

Fried, I., Katz, A., McCarthy, G., Sass, K.J., Williamson, P., Spencer, S.S., and Spencer, D.D. (1991). J. Neurosci. *11*, 3656–3666.

Fried, I., Mukamel, R., and Kreiman, G. (2011). Neuron *69*, this issue, 548–562.

Haggard, P. (2008). Nat. Rev. Neurosci. *9*, 934–946.

Kornhuber, H.H., and Deecke, L. (1965). Pflugers Arch. Gesamte Physiol. Menschen Tiere *284*, 1–17.

Lau, H.C., Rogers, R.D., Haggard, P., and Passingham, R.E. (2004). Science *303*, 1208–1210.

Libet, B., Gleason, C.A., Wright, E.W., and Pearl, D.K. (1983). Brain *106*, 623–642.

Matsuhashi, M., and Hallett, M. (2008). Eur. J. Neurosci. *28*, 2344–2351.

Picard, N., and Strick, P.L. (1996). Cereb. Cortex *6*, 342–353.

Sharp, D.J., Bonnelle, V., De Boissezon, X., Beckmann, C.F., James, S.G., Patel, M.C., and Mehta, M.A. (2010). Proc. Natl. Acad. Sci. USA *107*, 6106–6111.

Shima, K., and Tanji, J. (2000). J. Neurophysiol. *84*, 2148–2160.

Yazawa, S., Ikeda, A., Kunieda, T., Ohara, S., Mima, T., Nagamine, T., Taki, W., Kimura, J., Hori, T., and Shibasaki, H. (2000). Exp. Brain Res. *131*, 165–177.