

# Elucidating the neural circuitry underlying planning of internally-guided voluntary action

Michelle Marneveck and Véronique H. Flamand

Department of Biobehavioral Sciences, Teachers College, Columbia University, New York, New York

Submitted 22 January 2016; accepted in final form 24 April 2016

**Marneveck M, Flamand VH.** Elucidating the neural circuitry underlying planning of internally-guided voluntary action. *J Neurophysiol* 116: 2469–2472, 2016. First published April 27, 2016; doi:10.1152/jn.00068.2016.—In an attempt to elucidate the neural circuitry of planning of internally guided voluntary action, Ariani et al. (2015) used a delayed-movement design and multivariate pattern analysis of functional MRI data and found areas decoding internally elicited action plans, stimulus-elicited action plans, and both types of plans. In interpreting their results in the context of a heuristic decision model of voluntary action, encompassing “what” action to perform, “when” to perform it, and “whether” to perform it at all, we highlight at least some neural dissociation of these components. More to that, we note that the exact neural circuitry of each component might vary depending on the performed action type, and finally, we underscore the importance of understanding the temporal specifics of such circuitries to further elucidate how they are involved and interact during voluntary action planning.

motor planning; multivariate pattern analysis; voluntary action; decision

TO VOLUNTARILY CONTROL OUR OWN actions, or to “act as we choose” with intent is a unique feature of human behavior that allows the achievement of desired goals in day-to-day life. Although the neural circuitry of executing a voluntary internally guided action has been studied extensively, that of planning a voluntary action has received much less attention and remains a major unresolved question.

Generally, voluntary action, and its preparation, has been a difficult and controversial topic to study from an experimental perspective. In part, this has been due to a difficulty in coming up with an operationalized definition, especially given the arguably experimental intractability of “internal causes” of behavior (Nachev and Hussain 2010). Many who have attempted to elucidate the neural circuitry of voluntary action have done so by differentiating it from that of external stimulus-elicited, instructed actions. This approach, however, has its shortcomings in that asking someone to perform an action voluntarily is rather paradoxical, and asking someone to perform an action by instruction is not entirely involuntary (Haggard 2008). Nevertheless, as Haggard noted, such studies have highlighted an important feature of voluntary action, namely, that the individual must generate the information that is needed to perform an action; in other words, it has to be endogenously or internally computed or planned.

Despite the above-mentioned limitations, a large number of imaging studies (see Kriegerhoff et al. 2011 for review) have

compared situations in which participants freely choose an action with situations in which a stimulus determines an action. Some study findings have fitted with a broad distinction proposed by Goldberg (1985) in the neural circuitry of voluntary and stimulus-elicited actions, with the involvement of the frontomedian cortex in the former and the frontolateral cortex in the latter. However, there is not yet a consistent picture of specific regions that allow voluntary action, due to mixed results on the involvement of regions within the frontomedian wall. What might contribute to these mixed results?

Voluntary action has often been treated as a unitary concept, even though experimental studies might have focused on any number of different components of voluntary action (Haggard 2008). To this end, some have highlighted the importance of understanding and distinguishing components of voluntary action in previous and future work (e.g., Bestmann and Duque, in press; Brass and Haggard 2008; Cisek 2012). For example, Brass and Haggard (2008) identified three decision components that contribute to voluntary action: deciding “what” action to perform, deciding “when” to perform it, and deciding “whether” to perform it at all. Bestmann and Duque (in press) name the following components to be involved in planning of voluntary action: 1) conflict processing, that is, resolving which action to choose among a set of possible alternatives, 2) impulse control, that is, preventing actions from being performed too early, and 3) a type of inhibition that suppresses irrelevant information and monitors unexpected changes in our environment that demand modifying the action plan. It might be argued that these different terms describe the same overall processes. For example, the process of selecting what action to perform requires resolving which action to choose among a set of alternatives. Nevertheless, these different models highlight the multiplicity of processes that come into play in voluntarily planning an action. Furthermore, evidence is building for the “what, when, and whether” decision components of voluntary action to be to some extent dissociable on a neural level (see Kriegerhoff et al. 2011). Another explanation for mixed findings on the neural circuitry of voluntary action relates to voluntary action being studied using a number of different action types or movements, e.g., reaching, grasping, finger tapping. Many have pointed to some level of neural dissociation between different actions, that is, at least when they are stimulus-elicited (e.g., see Culham and Valyear 2006 for review; Cavina-Pratesi et al. 2010; Di Bono et al. 2015). Thus, it is conceivable that mixed findings are due to studying voluntary action using different action types, each of which carries their own unique neural circuitry. Finally, most studies on voluntary action have not separated execution of voluntary action from planning of voluntary action, which are two different phases of

Address for reprint requests and other correspondence: M. Marneveck, Dept. of Biobehavioral Sciences, Teachers College, Columbia Univ., 525 West 120th St., Box 93, New York, NY 10027 (e-mail: michellemarneveck.work@gmail.com).

motor control. That these two processes have not been isolated in studies of voluntary action incorrectly rests on the assumption that planning can be inferred from movement execution and that these processes have the exact same underlying neural circuitry.

Ariani et al. (2015) conducted a study in an attempt to address some of the above-mentioned limitations. Specifically, their use of a delayed-movement paradigm allowed for isolating planning from execution of voluntary action. To further explore what their study adds to our understanding of the neural circuitry of voluntary action planning, we first interpret their results in light of the what, when, and whether decision components of the Brass and Haggard (2008) model and the type of action captured by their design. We also discuss how the work by Ariani et al. (2015), and that of others who have isolated planning from execution of voluntary action, suggests at least some neural dissociation of different components of voluntary action planning, each of which might vary depending on the action type. Finally, we underscore the importance of understanding the temporal specifics of identified neural circuitries to further elucidate how they are involved and interact during voluntary action planning.

Using multivariate pattern analyses of functional magnetic resonance imaging (fMRI) data, Ariani et al. (2015) sought to distinguish between regions that generalize across planning of both voluntary and stimulus-elicited actions from regions that represent planning of voluntary actions and regions that represent planning of stimulus-elicited actions. They used a delayed-movement paradigm whereby, following a visual cue, subjects were asked to plan one of three reach-to-grasp actions (precision, whole hand, and touch) during a delay period and then, following an auditory cue, to execute the planned action within a specified time window. For the stimulus-elicited condition, different color cues corresponded to each movement type to be performed, and for the voluntary condition, the cue always had the same noninformative color. Thus the stimulus-elicited condition constrained, whereas the voluntary action condition did not constrain, what action to perform. Both conditions constrained when and whether to act (i.e., subjects had no free choice with regard to these decision components). Results showed contralateral parietofrontal regions, including contralateral primary motor cortex (M1) and dorsal premotor cortex (PMd), containing movement plans that were invariant to the way they were selected (voluntarily and stimulus-elicited). That these regions decoded both types of actions in a similar way suggests that they are important for action planning, regardless of how it was selected. Ariani et al. also found regions that preferentially represented voluntary selection of movements, namely, contralateral dorsolateral prefrontal cortex, ventral premotor cortex, and supramarginal gyrus, as well as ipsilateral posterior intraparietal sulcus and posterior superior and middle temporal gyrus. This suggests the distinct involvement of these regions in the planning of voluntarily selecting “what” action to perform. Neural circuitries of the other decision components of the Brass and Haggard (2008) model have also been explored in recent work on voluntary action planning. For example, the “whether” component of voluntary action planning has been shown to be decoded in a large network of regions within the bilateral parietal and lateral prefrontal cortex, including presupplementary motor area (Schel et al. 2014), and the “when” component of voluntary

action planning has been shown to be decoded in the supplementary motor area (SMA; Fried et al. 2011). Krieghoff et al. (2009) also highlighted the involvement of two different regions in deciding what action to perform (e.g., rostral cingulate zone, RCZ) and when to perform it (e.g., superior frontal gyrus, paramedian frontal cortex).

The above-described work demonstrates the involvement of neuroanatomically dissociable regions for different decision components in generating voluntary actions within the fronto-median wall. However, regions underlying a certain component of voluntary action planning might vary depending on the type of action. For example, the study by Krieghoff et al. (2009) highlighted the involvement of RCZ for the decision of what button to press in a button-press task. This area was not highlighted by Ariani et al. (2015) as a region involved in the planning of what action to perform (precision or whole hand grasp or touch). Many studies of stimulus-elicited actions have documented some level of neural dissociation during execution of different types of action (reach vs. grasp: see Culham and Valyear 2006 for review; Cavina-Pratesi et al. 2010; stimulus-elicited precision vs. whole hand grasp: e.g., Begliomini et al. 2007; Di Bono et al. 2015). It is conceivable too that there might in part be some neural discrepancies between planning of different types of voluntary actions. Thus the neural signature of voluntary action planning varies not only depending on the decision component involved but also depending on the action type to be performed (e.g., button press vs. grasp type). This might in part explain discrepancies between regions identified in Ariani et al. (2015) during planning of grasp types and regions identified by other studies, such as that by Krieghoff et al. (2009) during planning of button press/finger tapping.

What also renders some of Ariani et al.’s (2015) results difficult to interpret in light of the literature is that many previous imaging studies on voluntary action do not distinguish in their designs between planning and execution of voluntary action. For example, Ariani et al. discuss the result of involvement of SMA in stimulus-elicited action planning to be in contrast with others, such as Lau et al. (2004), who showed involvement of SMA in voluntary action planning. However, Lau et al. (2004) did not measure planning of voluntary action, but inferred it from execution of voluntary action. The delayed-movement fMRI paradigm used by Ariani et al. (2015) did well in separating the processes involved in planning from the processes involved in execution of voluntary action. With this design, they have demonstrated a network of regions specifically involved in voluntarily selecting grasp actions during a period of time before object grasping.

As a final point, the evidence discussed in Ariani et al. (2015) for the role of each of the identified neural regions in planning of voluntary actions, compared with stimulus-elicited actions, is for the most part limited to neuroimaging studies. The use and report of neurophysiological studies on this topic will give a refined understanding by showing not only which regions are involved in voluntary action planning but also how they are involved. The noninvasive study of preparatory cortical activity by multichannel high-resolution EEG has identified numerous components of movement-related cortical potentials that are recorded at specific time points before movement onset, which relate to movement planning (see Shibasaki and Hallett 2006 for review). For example, the contingent-

negative variation (CNV) is thought to reflect neuronal activity during preparation of stimulus-elicited actions, whereas the Bereitschaftspotential (BP) is thought to reflect neuronal activity during preparation of voluntary actions. Recently, it was shown that repetitive transcranial magnetic stimulation (rTMS) over PMd increased CNV (and not BP), whereas rTMS over SMA increased BP (but not CNV) occurring 0 to 500 ms before movement onset (Lu et al. 2012). This provides direct evidence for the role of PMd in planning of stimulus-elicited actions rather than voluntary actions and for the role of SMA in planning of voluntary actions rather than stimulus-elicited actions. It is likely that the activity captured by Lu et al. (2012) 0 to 500 ms before movement onset might not have been captured in Ariani et al.'s (2015) movement delay period and occurs only following the "go" signal. Nevertheless, such temporally specific modulation of PMd and SMA in stimulus-elicited and voluntary actions, respectively, would not be captured in an imaging-based analysis given its limitation for temporal specificity. Similarly, using temporal measures such as TMS to study M1 modulation might reveal temporally specific differences between voluntary and stimulus-elicited action plans (which were not revealed in Ariani et al. 2015). Modulation of M1 during motor planning following a "go" cue but shortly before movement onset is well established: specifically, there is an increase in excitability of M1 ~100 ms before movement onset (Chen and Hallett 1999), which is likely mediated by a decrease in intracortical inhibition (Reis et al. 2008; Reynolds and Ashby 1999). M1 modulation during motor planning before a "go" cue has also been demonstrated, with excitability being suppressed in anticipation of an expected "go" signal leading to action (Duque et al. 2010). This latter modulation has been related to an inhibitory process exerting its influence during a delay period, preventing the premature release of action (Bestmann and Duque, in press). To our knowledge, the above work showing M1 modulation relating to prevention of prematurely released actions has mostly been studied using stimulus-elicited actions. It is possible that TMS measures would show differential M1 modulation depending on the action being selected voluntarily or externally, at least in the way it was measured by Ariani et al. (2015). In their voluntary condition, subjects were required to select an action between three possible alternatives and then prepare the chosen action during the delay period. During the same delay period, in their stimulus-elicited action condition, subjects knew as soon as the informative cue was presented what action to prepare. It is conceivable that similar mechanisms modulating M1 excitability come into play in both conditions while the upcoming action is being planned, but at different time points relative to the "go" cue. Incorporating TMS in a delayed-movement design contrasting both action types, such as that of Ariani et al. (2015), would allow identification of the suggested differences in temporally specific M1 modulation during voluntary and stimulus-elicited action planning. Finally, although it is useful to identify the role of neural regions involved in each of the components of voluntary action planning, what seems pertinent is the study of functional interactions between these regions. This sort of work is more in its infancy than fMRI work but is already underway. For example, one study by Nguyen et al. (2014) has shown, using an integrative EEG-fMRI approach, a strong

reciprocal connection between SMA and cingulate cortex during voluntary action planning.

The work by Ariani et al. (2015) has extended our understanding of the neural bases of voluntary action planning by demonstrating the involvement of neural regions in voluntary selection of grasp and touch actions before its execution. The temporal specifics and interaction within this network of regions and between regions that decode other components of voluntary action planning remain an important ongoing avenue for investigation.

#### GRANTS

M. Marneveck is supported by an Endeavour Australia Research Fellowship. V. H. Flamand is supported by Fonds de la Recherche en Santé du Québec Postdoctoral Training Award.

#### DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

#### AUTHOR CONTRIBUTIONS

M.M. and V.H.F. conception and design of research; M.M. and V.H.F. analyzed data; M.M. and V.H.F. interpreted results of experiments; M.M. and V.H.F. drafted manuscript; M.M. and V.H.F. edited and revised manuscript; M.M. and V.H.F. approved final version of manuscript.

#### REFERENCES

- Ariani G, Wurm XM, Lingnau A. Decoding internally and externally driven movement plans. *J Neurosci* 35: 14160–14171, 2015.
- Begliomini C, Wall MB, Smith AT, Castiello U. Differential cortical activity for precision and whole-hand visually guided grasping in humans. *Eur J Neurosci* 25: 1245–1252, 2007.
- Bestmann S, Duque J. Transcranial magnetic stimulation: decomposing the processes underlying action preparation. *Neuroscientist*. In press.
- Brass M, Haggard P. The what, when, whether model of intentional action. *Neuroscientist* 14: 319–325, 2008.
- Cavina-Pratesi C, Monaco S, Fattori P, Galletti C, McAdam TD, Quinlan DJ, Goodale MA, Culham JC. Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. *J Neurosci* 30: 10306–10323, 2010.
- Chen R, Hallett M. The time course of changes in motor cortex excitability associated with voluntary movement. *Can J Neurol Sci* 26: 163–169, 1999.
- Cisek P. Making decisions through a distributed consensus. *Curr Opin Neurobiol* 22: 927–936, 2012.
- Culham JC, Valyear KF. Human parietal cortex in action. *Curr Opin Neurobiol* 16: 205–212, 2006.
- Di Bono MG, Begliomini C, Castiello U, Zorzi M. Probing the reaching-grasping network in humans through multivoxel pattern decoding. *Brain Behav* 5: e00412, 2015.
- Duque J, Lew D, Mazzocchio R, Olivier E, Ivry RB. Evidence for two concurrent inhibitory mechanisms during response preparation. *J Neurosci* 30: 3793–3802, 2010.
- Fried I, Mukamel R, Kreiman G. Internally generated preactivation of single neurons in human medial frontal cortex predicts volition. *Neuron* 69: 548–562, 2011.
- Goldberg G. Supplementary motor area structure and function: review and hypotheses. *Behav Brain Sci* 8: 567–616, 1985.
- Haggard P. Human volition: towards a neuroscience of will. *Nat Rev Neurosci* 9: 934–946, 2008.
- Kriehoff V, Brass M, Prinz W, Waszak F. Dissociating what and when of intentional actions. *Front Hum Neurosci* 3: 1–10, 2009.
- Kriehoff V, Waszak F, Prinz W, Brass M. Neural and behavioral correlates of intentional actions. *Neuropsychologia* 49: 767–776, 2011.
- Lau HC, Rogers RD, Ramnani N, Passingham RE. Willed action and attention to the selection of action. *Neuroimage* 21: 1407–1415, 2004.
- Lu MK, Arai N, Tsai CH, Ziemann U. Movement related cortical potentials of cued versus self-initiated movements: double dissociated modulation by

- dorsal premotor cortex versus supplementary motor area rTMS. *Hum Brain Mapp* 33: 824–839, 2012.
- Nachev P, Husain M.** Action and the fallacy of the “internal”: comment on Passingham et al. *Trends Cogn Sci* 14: 192–194, 2010.
- Nguyen VT, Breakspear M, Cunnington R.** Reciprocal interactions of the SMA and cingulate cortex sustain premovement activity for voluntary actions. *J Neurosci* 34: 16397–16407, 2014.
- Reis J, Swayne OB, Vandermeeren Y, Camus M, Dimyan MA, Harris-Love M, Perez MA, Ragert P, Rothwell JC, Cohen LG.** Contribution of transcranial magnetic stimulation to the understanding of cortical mechanisms involved in motor control. *J Physiol* 586: 325–351, 2008.
- Reynolds C, Ashby P.** Inhibition in the human motor cortex is reduced just before a voluntary contraction. *Neurology* 53: 730–735, 1999.
- Schel MA, Kuhn S, Brass M, Haggard P, Ridderinkhof KR, Crone EA.** Neural correlates of intentional and stimulus-driven inhibition: a comparison. *Front Hum Neurosci* 8: 27, 2014.
- Shibasaki H, Hallett M.** What is the Bereitschaftspotential? *Clin Neurophysiol* 117: 2341–2356, 2006.

