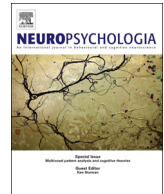




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The kinematic signature of voluntary actions

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ABSTRACT

Research in the field of psychology and cognitive neuroscience has begun to explore the functional underpinnings of voluntary actions and how they differ from stimulus-driven actions. From these studies one can conclude that the two action modes differ with respect to their neural and behavioural correlates. So far, however, no study has investigated whether the voluntary and stimulus-driven actions also differ in terms of motor programming. We report two experiments in which participants had to perform either voluntary or stimulus-driven reach-to-grasp actions upon the same stimulus. Using kinematic methods, in Experiment 1 we obtained evidence that voluntary actions and stimulus-driven actions translate into differential movement patterns. Results for Experiment 2 suggest that selecting what to do, when to act, and whether to act are characterized by specific kinematic signatures and affect different aspects of the reach-to-grasp movement in a selective fashion. These findings add to current models of volition suggesting that voluntary action control results from an interplay of dissociable subfunctions related to specific decision components: *what* action execute, *when* to execute an action, and *whether* to execute any action.

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1. Introduction

Voluntary actions have been proposed to lie at one end of a continuum that has stimulus-driven actions at the other end (Haggard, 2008). Whereas the form, timing, and occurrence of stimulus-driven actions are determined by an identifiable external stimulus, voluntary actions are not directly determined – or, at least, not entirely determined (Schüür and Haggard, 2011) – by an external stimulation, but reflect a *decision* process.

Studies using both event-related potentials (ERPs; e.g., Waszak et al., 2005) and functional imaging (e.g., Jenkins et al., 2000) suggest that voluntary control and stimulus-driven control are mediated by neurophysiologically and functionally distinct routes: while stimulus-driven actions are controlled via a lateral network including the parietal and premotor cortex, voluntary control involves the fronto-median cortex (for review, see Kriegerhoff et al., 2011). However, since both routes converge in a final common pathway, it is not clear whether these two types of actions are also implemented at a motor level differently.

In this respect, Waszak and colleagues (2005) report that the response-locked RP (readiness potential, a movement-related cortical potential that reflects preparation to response and is measured over medial frontal structures) occurred earlier and was more negative for voluntary actions than for stimulus-driven actions. The response-locked LRP (lateralized readiness potential), which represents increased cortical activity contralateral to the forthcoming response and is thought to reflect specific motor preparation, however, remained essentially invariant for stimulus-driven and voluntary actions. This result was taken to suggest that the specific motor programming did not differ between the two conditions. Other studies contrasting voluntary and stimulus-driven actions have similarly assumed that, despite being controlled by different neural networks, the movements in the two modes of action are the same (Astor-Jack and Haggard, 2005; Cunnington et al., 2002). Very little empirical work, however, has directly tested whether voluntary and stimulus-driven control do lead to the same or different motor outputs.

1.1. Decisions in the motor system

The notion that motor programming is the same for voluntary and stimulus-driven control is consistent with traditional

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information-processing models of decision making, assuming that the process of deciding is complete before the motor system is brought into play (Donders, 1868/1969; Sternberg, 1969). According to these models, cognitive processing would lead to a decision and the outcome would then be passed to the motor system to be converted into action. Because the motor system is recruited only after the decision outcome is complete, these sequential models leave little room for the motor system to play an ongoing role in the decision process itself (Kubaneck and Kaplan, 2012).

The strict separation between the cognitive system and the motor system is well suited to the problem-solving tasks in which the relevant contingencies are purely abstract. In the natural environment, however, decision alternatives are often associated with actions and it is plausible that sensorimotor control is engaged in parallel with evaluating different options (Cisek, 2012). In this view, recent accounts suggest that the processes of *action selection* (i.e., selection between action alternatives that are currently possible) and *action specification* (i.e., specification, at the motor level, of the parameters or metrics of those actions) occur simultaneously and continue even during overt performance of movements (Cisek, 2007). In this perspective, motor structures may have a role in decision formation, contributing to the evaluation of different alternative options (Cisek, 2006, 2007, 2012; Friston, 2008; Shalden et al., 2008; Cisek and Kalaska, 2010). Support for this notion comes from the finding that decisions influence the competition between action representations in motor cortex before the decision process is complete (Selen et al., 2012; Klein-Flügge and Bestmann, 2012). For example, it has been demonstrated that when subjects make *perceptual decisions* using arm movements, their arm reflex gains are changed in parallel with the decision variable that explains their choice behaviour, as if decision processes change the arm's preparatory state at the corticospinal level (Selen et al., 2012). This has been taken to suggest that decision processes can spill into the motor system and influence the way the motor system chooses and implements movements (Cisek, 2012; Doya and Shalden, 2012). On this account, decisions about impending actions – including the various component decisions that lead up to the performance of a voluntary action – may be expected to be continuously reflected in many aspects of the motor system, including the specific features of ongoing movements.

According to the *what, whether, when* model, three component decisions are critical to voluntary action (Brass and Haggard, 2008; Haggard, 2008): a component related to action selection, i.e., to the decision about which action to perform (*what* component); a component about whether to perform the selected action (*whether* component); and finally, a component related to action timing, i.e., to the decision about when to perform the selected action (*when* component). It has been demonstrated that *what, whether, and when* decision components related to different neural processes, occurring in different regions of the brain (Krieghoff et al., 2011). To the best of our knowledge, however, no study has investigated whether these different decision components also exert a *specific* influence on motor planning and execution.

1.2. Measuring voluntary motor control

Initial evidence that motor programming differs between the voluntary and the stimulus-driven mode was provided by Obhi and Haggard (2004). By measuring electromyographic response (EMG) from the first dorsal interosseus, these authors demonstrated that free timing finger key presses – which can be considered to be product of a *when* decisions – elicited significantly greater muscle activation than externally triggered finger presses. When preparation of the voluntary movement was truncated by an external stimulus requiring the same motor

response than that the subject was already preparing, and participants were therefore forced to switch from a voluntary mode of response to an externally triggered mode, reaction time was delayed. This suggests that the motor system cannot take advantage of preexisting levels of motor preparation. Interestingly, the basic characteristics of EMG signatures of internally and externally generated presses were preserved in truncation, suggesting that participants were indeed switching between the two modes of action control rather than modifying the ongoing action. Other studies using similar paradigms, however, failed to show interference. Rather they reveal an overlap of voluntary and stimulus-driven action preparation. For example, Hughes et al. (2011) found that voluntary motor preparation, measured by RPs amplitude, was partially transferable to stimulus-driven action preparation, suggesting that the two routes to action may converge on a common preparatory mechanism. The question remains therefore open as to whether the motor system processes voluntary and stimulus-driven actions separately. Moreover, it is not clear whether and to what extent different decision components may contribute to action specification.

Experimental designs such as the ones described examine the relation between voluntary and stimulus-driven actions by testing whether preparatory activity in one system is transferable to the other when 'switch to' actions are exactly the same (Obhi et al., 2008). Reaction times as well as EMG alone, however, may be insufficient to determine whether *exactly the same movements* are performed in the two modes of control. If not, this may provide evidence that motor control of voluntary and stimulus-driven action is indeed different (Glover, 2004). An alternative approach to investigate whether voluntary and stimulus-driven actions are independent or overlap is thus to examine the detailed spatio-temporal pattern of movement kinematics in the two modes.

Following this approach, the present study was designed to investigate whether and how voluntary decisions shape the kinematics of reach-to-grasp movements. Specifically, we wanted to determine i) how voluntary control impacts on the execution of a reach-to-grasp movement; ii) to what extent specific decision components contribute to the kinematic patterning of voluntary and stimulus-driven movements. To this end, we employed a paradigm that while maintaining direct comparability of voluntary and stimulus-driven movements, allowed comparison of the kinematic signature of *what, when, and whether* decision components. In two experiments, participants were asked to perform either voluntary or stimulus-driven reach-to-grasp movements upon a large or a small object. In Experiment 1, participants were free to decide what action to perform, whether to act, and when to do so. In Experiment 2, *what, whether, and when* decision components were dissociated and independently manipulated to clarify the differential contribution of each component to movement kinematics.

2. Experiment 1

In Experiment 1, participants were asked to reach towards and grasp one of two objects (small vs. large) under either a 'constrained' or a 'voluntary' condition. For the 'constrained' condition, the action sequence was entirely predetermined. Participants were instructed regarding which object to grasp, whether to perform the action, and when to perform the action. In the 'voluntary' condition, participants freely choose what action to perform, as well as whether and when to perform it. The reach-to-grasp movement towards large and small objects has been well characterized experimentally under constrained conditions (e.g., Gentilucci et al., 1991; Jakobson and Goodale, 1991). Despite its

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