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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 Experiments 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.

Keywords: voluntary actions, stimulus-driven actions, kinematics, reach-to-grasp, motor control

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 & Haggard, 2011) – by an external stimulation, but reflect a *decision* process.

Studies using both event-related potentials (ERPs; e.g., Waszak, Wascher, et al., 2005) and functional imaging (e.g., Jenkins, Jahanshani, Jueptner, Passingham, & Brooks, 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-medial cortex (for review, see Kriehoff, Waszak, Prinz, & Brass, 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 & Haggard, 2005; Cunnington, Windischberger, Deecke, & Moser, 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 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 (Kubanek & 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, Kiani, Hanks, & Churchland, 2008; Cisek & Kalaska, 2010). Support for this notion comes the finding that decisions influence the competition between action representations in motor cortex before the decision process is complete (Selen, Shadlen, & Wolpert, 2012; Klein-Flügge & Bestmann, 2012). For example, it has been demonstrated that when subjects make *perceptual decisions* using arm movements, their arm reflex gains is changed in parallel with the decision variable that explains their choice behaviour, as if decision process 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 & Shadlen, 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 & 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 for 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 interosseous, 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, Schütz-Bosbach, & Waszak (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, Matkovich, & Gilbert, 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 (eg, Gentilucci et al., 1991; Jakobson & Goodale, 1991). Despite its simplicity, it can therefore assist in the differentiation of the two modes of action.

If voluntary and stimulus driven control are independent, we would predict that the kinematics of voluntary reach-to-grasp movements would differ from the kinematics of constrained reach-to-grasp movements aimed at the same target object (small vs. large). Differences in the reach-to-grasp kinematic patterning for the same object have been demonstrated depending on the action end goal and intention (e.g. Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Ansuini, Santello, Massaccesi, & Castiello, 2006; Becchio, Sartori, Bulgheroni, & Castiello, 2008a; Becchio, Sartori, Bulgheroni, & Castiello, 2008b; Georgiou, Becchio, Glover, & Castiello, 2007). For example, movement duration is longer, amplitude of maximum grip aperture is lower and is reached earlier in time when the object is used to cooperate with a partner in comparison to when it used to compete against an opponent (Georgiou et al., 2007; Becchio et al., 2008b). Along similar lines, intentional attitudes have been shown to influence key grasping parameters, such time of peak grip

opening and closing velocity (Sartori, Becchio, & Castiello, 2011). We reasoned that if voluntary control differs from stimulus driven control, then differences in kinematic parameters concerned with both the reaching and the grasping component should be observed for movements aimed at the same object. Alternatively, if the two systems overlap, we would expect the two modes of actions to be characterized by a similar kinematic patterning.

2.1. Methods

2.1.1. Participants

Thirteen subjects (6 females) between 18 and 30 years (female mean age = 21.67 years, SD = 1.21 years; male mean age = 23.71 years, SD = 3.55 years) participated in the study. One participant was excluded from the final analyses due to abnormal motor performance (bradykinesia) as compared to the other participants. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Participants were naïve as to the purpose of the investigation and gave informed written consent to participate in the study. The local Institutional Review Board of the University of Padua in accordance with the Declaration of Helsinki approved the experimental procedures.

2.1.2. Stimuli

The manipulandum consisted of a small cylinder (height 14 cm, diameter 1.5 cm; Figure 1a) inserted within a larger cylindrical base (height 11 cm, diameter 7.5 cm; Figure 1a). The small and large cylinders could be grasped with a precision and power grip, respectively (Figure 1b, c). In order to exclude that the greater height of the smaller cylinder might have determined differences in spatial trajectories for the index finger and thumb, a preliminary analysis on the y component concerned with the movements of these two digits was performed. No significant differences were detected. For the sake of clarity from now on we shall refer to the small part of the manipulandum as ‘small object’ and to the large part of the manipulandum as ‘large object’.

Insert Figure 1 about here

2.1.3. Apparatus

Movements were recorded by means of a three-dimensional motion analysis system (SMART-D; BTS, Garbagnate Milanese, Italy) equipped with six infrared cameras (frequency: 140 Hz). Reflective passive markers (diameter = 0.25 cm) were fastened using double-sided tape to (a) the wrist, (b) the tip of the index finger, (c) the tip of the thumb of the participants' right hand, and (d) on the top of the visual stimuli. The wrist marker was used to measure the reaching component of the action. The markers positioned on the index finger and the thumb were used to measure the grasp component of the action. Coordinates of the markers were reconstructed with an accuracy of 0.2 mm over the field of view. The standard deviation of the reconstruction error was 0.2 mm for both the vertical (Y) and horizontal (X and Z) axes. Data were reconstructed, filtered (10 Hz), and analyzed by means of the SMART-D analyzer software.

2.1.4. Procedure

Participants sat at a table with their right hand on a starting platform. A pressure sensitive switch was embedded in the starting platform so that when the reaching movement towards the target commenced, the switch was released indicating the movement onset. Movement offset was calculated as the time at which the object was lifted from the working surface for two consecutive frames (14 ms). The manipulandum was aligned with the participant's body midline and located at a 35-cm distance from the hand starting position. Participants were instructed to reach towards and grasp the designated part of the manipulandum in two experimental conditions: a 'constrained' and a 'voluntary' condition. For the 'constrained' condition, the action sequence was entirely predetermined. Before the beginning of each trial, the participants were instructed to grasp either the large or the small object. Prior of trial onset, one of two possible auditory informed participants

whether or not an action had to be performed: a low-pitch tone (Hz = 400; duration = 300 ms) indicated that no action had to be performed, whereas a high-pitched tone (Hz = 700; duration = 300 ms) signalled that the action should be executed. In this latter case, a second tone (Hz = 550; duration = 70 ms) randomly delivered between 2000 and 2500 ms after the first tone indicated when the action should start. Each participant performed 27 trials for each type of object (21 Go trials; 6 No Go trials). This resulted in a total of 54 trials. In the 'voluntary' condition, participants were asked to freely select what action to make, whether to make it, and when to make it. After the presentation of a tone (Hz = 550; duration = 70 ms), they were given a 5s time window to decide which object to grasp, whether to perform the action, and when to start their movement. Each participant performed 15 movements towards the large object and 15 movements towards the small object, for a total amount of 60 trials. The order of conditions was randomized across participants. Participants underwent a practice session before the experimental session commenced.

2.1.5. Dependent variables and data analysis

To test for possible differences in the kinematics of the reach-to-grasp movement as a function of experimental conditions a repeated measures analysis of variance (ANOVA) with 'Condition' (constrained, voluntary) and 'Object Size' (large, small) as within-subjects factors was conducted. Simple effects were used to explore the means of interest and Bonferroni corrections (alpha level: $p < .05$) were applied when necessary. The statistical analysis considered key reach-to-grasp kinematic landmarks, which are known to vary depending on movement speed (e.g., Wing, Turton, & Fraser, 1986) and action intention (Becchio et al., 2008a; Becchio et al., 2008b; Georgiou et al., 2007; Sartori, Becchio, Bulgheroni, & Castiello, 2009; Sartori et al., 2011). These included: (i) movement duration, calculated as the time between the release of the starting switch and the closure of the fingers around the object; (ii) amplitude of maximum grip aperture, corresponding to the maximum distance reached by the thumb and index finger during the unfolding of the action; (iii) time of maximum grip aperture, calculated as the point in time at which index finger and thumb

reached the of maximum distance; (iv) time of peak grip opening velocity, corresponding to the point in time at which the velocity of distancing the thumb and the index finger reached its maximum value; and (v) time of peak grip closing velocity, indicating the point in time at which the velocity of thumb-index finger during the closing phase reached its maximum value. In addition to these measures, we also considered (vi) delay between the start of the reaching action and the initiation of fingers opening. This variable was analyzed to quantify the coordination between the reach and the grasp component at movement start. Lastly, we measured (vii) movement onset, calculated as the time between the presentation of the tone (second tone for the ‘constrained’ condition) and the release of the starting switch.

2.2. Results and discussion

The repeated measures ANOVA revealed a significant main effect of ‘Condition’ for movement onset, $F(1,12) = 11.273$; $p < .01$, $\eta_p^2 = .484$, movement duration, $F(1,12) = 28.22$, $p < .0001$, $\eta_p^2 = .720$, time of maximum grip aperture, $F(1,12) = 23.13$, $p < .001$, $\eta_p^2 = .678$, time of peak grip opening velocity, $F(1,12) = 10.60$, $p < .01$, $\eta_p^2 = .491$, and time of peak grip closing velocity, $F(1,12) = 28.60$, $p < .0001$, $\eta_p^2 = .722$. Movement onset was anticipated for the ‘constrained’ compared to the ‘voluntary’ condition (518 ± 36 vs. 628 ± 62 ms). Movement duration was significantly longer for the ‘constrained’ than for the ‘voluntary’ condition (1121 ± 132 vs. 972 ± 106 ms). Maximum grip aperture was reached later in time for the ‘constrained’ compared to the ‘voluntary’ condition (699 ± 82 vs. 577 ± 64 ms). Similarly, time of peak velocity of grip opening and grip closing occurred later for the ‘constrained’ than for the ‘voluntary’ condition (392 ± 35 vs. 288 ± 33 ms and 898 ± 95 vs. 769 ± 85 ms, respectively). The main effect of ‘Object Size’ was significant for movement duration, $F(1,12) = 32.26$, $p < .0001$, $\eta_p^2 = .746$, amplitude of maximum grip aperture, $F(1,12) = 146.54$, $p < .0001$, $\eta_p^2 = .993$, time of maximum grip aperture, $F(1,12) = 13.17$, $p < .005$, $\eta_p^2 = .545$, time of peak grip opening velocity, $F(1,12) = 40.11$, $p < .01$, $\eta_p^2 = .785$, time of peak grip closing velocity, $F(1,12) = 10.24$, $p < .001$, $\eta_p^2 = .482$, and delay, $F(1,12) = 25.27$,

$p < .0001$, $\eta_p^2 = .697$. Movement duration was shorter for the large than for the small object (991 ± 102 vs. 1102 ± 142 ms). As expected, maximum grip aperture was wider (119 ± 8 vs. 63 ± 5 mm) and it was reached later in time (695 ± 75 vs. 581 ± 49 ms) for the large compared to the small object. Both time of peak grip opening and closing velocity occurred earlier for the small compared to the large object (302 ± 40 vs. 378 ± 42 ms, and 780 ± 84 vs. 886 ± 93 ms, respectively). Delay was significantly reduced for movements aimed at the large than the small object (177 ± 22 vs. 280 ± 31 ms). A significant two-way interaction ‘Condition’ by ‘Object Size’ was found for time of peak grip closing velocity, $F(1,12) = 8.57$, $p < .05$, $\eta_p^2 = .438$. For the voluntary condition, peak velocity for grip closing was reached earlier for the small than for the large object (851 ± 91 vs. 686 ± 76 ms). No such difference was detected for the constrained condition (920 ± 104 vs. 875 ± 93 ms, $p > 0.05$).

In sum, these findings indicate that voluntary and stimulus-driven control led to different motor outputs. This suggests that over and above the effect of object size, the mode of control – voluntary versus stimulus-driven – specifically influenced the motor programming of reach-to-grasp movements, contributing to action specification.

3. Experiment 2

The result of Experiment 1 showed that the kinematics of reach-to-grasp movements is different depending on whether the determination of which action to perform, whether and when to perform it is voluntary or constrained. To clarify the contribution of specific decision components to movement kinematics, in Experiment 2, we independently constrained *what*, *whether*, and *when* components.

3.1. Method

3.1.1. Participants

Fourteen participants (7 females; (female mean age = 24.43 years, SD = 2.51 years; male mean age = 25.14 years, SD = 3.93 years) participated in the study. None of Experiment 2 participants took part in Experiment 1.

3.1.2. Stimuli, apparatus, and procedure

Stimuli, apparatus, and procedure were the same as those for Experiment 1, with the exception that there were four experimental conditions: ‘what constrained’, ‘whether constrained’, ‘when constrained’ and ‘voluntary’. In the ‘what constrained’ condition, prior to the beginning of each trial, participants were instructed to grasp either the large or the small object. They were free to decide whether to perform the action and, if they decided to act, when to grasp the object. After a tone (Hz = 550; duration = 70 ms) was presented, they had 5 s to decide whether and when to perform the action. In the ‘whether constrained’ condition participants were free to choose which object to grasp and when to start the movement, but whether to perform the action was dictated by an external cue. In this condition one of two possible auditory tones was randomly presented. A low-pitch tone (Hz = 400; duration = 300 ms) indicated that no action had to be performed, whereas a high-pitched tone (Hz = 700; duration = 300 ms) signalled that the action should be executed. After the high-pitched tone was presented, participants had 5 s to decide which object to grasp and when to start the action. In the ‘when constrained’ condition participants were free to decide which object to grasp and whether to perform the action, but not when to start the movement. In this condition a tone (Hz = 550; duration = 70 ms) indicated the onset of the trial. After a random interval (ranging from 1000 to 5000 ms), a second tone was presented (Hz = 550; duration = 70 ms). After hearing the second tone participants had 2 s to reach and grasp one of the two stimuli. For the ‘voluntary’ condition, as for Experiment 1, participants were asked to freely select what action to make, whether to make it, and when to make it. After the presentation of a tone (Hz = 550;

duration = 70 ms), participants were given 5 s to choose whether to perform or not the action, which object to grasp, and when to start their movement. Each participant performed 120 trials, 15 movements towards the large object and 15 movements towards the small object for each condition. The order of conditions was randomized across participants.

3.1.3. Dependent variables and data analysis

The same dependent variables described in Experiment 1 were considered. A repeated measures ANOVA with ‘Condition’ (voluntary, what constrained, whether constrained, when constrained), and ‘Object Size’ (large, small) as within-subjects factors was conducted. Simple effects were used to explore the means of interest and Bonferroni corrections (alpha level: $p < .05$) were applied when necessary.

3.2. Results and discussion

The main effect of ‘Condition’ was significant for movement onset, $F(3,39) = 7.062$, $p = .001$, $\eta^2 = .352$, movement duration, $F(3,39) = 3.53$, $p < .05$, $\eta^2 = .213$, and the time of maximum grip aperture, $F(3,39) = 4.57$, $p < .05$, $\eta^2 = .260$. Post-hoc contrasts indicated that movement onset was significantly anticipated for the ‘when constrained’ condition in comparison to the ‘whether constrained’ condition (631 ± 55 ms vs. 1075 ± 140 ms; $p = .011$). The differences between the ‘when constrained’ condition and the ‘voluntary’ (1151 ± 205 ms) and the ‘what constrained’ condition (964 ± 144 ms) were not significant, but there was a trend for time of action onset to be shorter in the ‘when constrained’ condition (respectively, $p = .062$ and $p = .056$). Movement duration was significantly longer for the ‘voluntary’ compared to the ‘what constrained’ and the ‘whether constrained’ conditions ($p_s < .05$; Fig. 2a). Maximum grip aperture was reached later in time for the ‘voluntary’ compared to the ‘what constrained’ and the ‘when constrained’ conditions ($p_s < .05$; Fig 2b).

The main effect of ‘Object Size’ was significant for movement duration, $F(1,13) = 57.24$, $p < .0001$, $\eta_p^2 = .815$, amplitude of maximum grip aperture, $F(1,13) = 553.58$, $p < .0001$, $\eta_p^2 = .977$, time of maximum grip aperture, $F(1,13) = 125.51$, $p < .0001$, $\eta_p^2 = .906$, time of peak grip velocity opening $F(1,13) = 43.85$, $p < .0001$, $\eta_p^2 = .771$, time of peak grip velocity closing, $F(1,13) = 88.60$, $p < .0001$, $\eta_p^2 = .872$, and delay, $F(1,13) = 25.38$, $p < .0001$, $\eta_p^2 = .661$. As expected, movement duration was shorter for the large than for the small object (818 ± 901 vs. 1006 ± 118 ms). Maximum grip aperture was wider (122 ± 105 vs. 62 ± 57 mm) and it was reached later in time (632 ± 73 vs. 437 ± 54 ms) for the large compared to the small object. The time of both peak grip opening and closing velocity occurred earlier for the small compared to the large object (204 ± 32 vs. 290 ± 43 ms, and 636 ± 75 vs. 800 ± 95 ms, respectively). The delay was significantly reduced when the large rather than the small object was grasped (151 ± 26 vs. 274 ± 39 ms). The two-way interaction ‘Condition’ by ‘Object Size’ was not significant for any of the considered dependent measures ($p_s > .05$).

Insert Figure 2 about here

All in all, these findings indicate that selecting what to do, when to act, and whether to act affect different aspects of the reach-to-grasp movement in a selective fashion. In particular, whereas *what* decisions affect both movement time and time to maximum grip aperture, *whether* decisions only influence movement time. Finally, *when* decisions appear to influence the time of maximum grip aperture, but not the overall movement duration.

4. General Discussion

The aim of the present research was to determine how voluntary and stimulus-driven control impact on action selection and specification. To do so, in two experiments we measured the kinematics of voluntary and constrained movements. In Experiment 1, we contrasted voluntary and stimulus-

driven reach-to-grasp movements performed upon a small or a large object. We found that some aspects of the kinematic patterning that characterizes reach-to-grasp movements aimed at large or smaller object changed depending on whether or not the action reflected a free decision. In Experiment 2, whether different decision components would influence the reach-to-grasp movement in a selective fashion was investigated. Kinematical analysis revealed that *what*, *whether*, and *when* decision components selectively affected different movement characteristics.

4.1. Voluntary vs. stimulus driven control

Experiment 1 showed that movement duration was longer and time of maximum grip aperture was reached later in time for ‘constrained’ movements in comparison to ‘voluntary’ movements. In Experiment 2, in contrast, we found that movement duration was longer for ‘voluntary’ movements in comparison to ‘what constrained’ and ‘whether constrained’ movements. Moreover, time of maximum grip aperture was reached later in time for ‘voluntary’ than for ‘what constrained’ and ‘when constrained’ movements. This suggests that the patterning found in Experiment 1 was not determined by a specific decision component, but rather reflected the need to integrate different components.

Under natural circumstances (i.e., when the target remains stationary), movement time is largely determined by planning processes operating prior to movement execution (Glover, 2004). In particular, planning is hypothesized to slow down movements made towards ‘hard’ targets (e.g., small targets) to allow for the control system more time to operate during action execution. One factor that in Experiment 1 could have influenced movement duration is task complexity. Research from a number of disciplines (e.g., accounting, finance, consumer behavior) has found that an increase in task demands decreases decision quality and increases the time required to make a decision (e.g., Hart, 1986). Similarly, task complexity has been shown to impact on movement planning, increasing movement duration (Meulenbroek, Van Galen, Hulstijn, Hulstijn, & Bloemsaat, 2004)

In Experiment 1, before the beginning of each trial, participants were instructed to grasp either the large or the small object. Then, two tones were administered in sequence. The first tone specified whether or not an action had to be performed. The second tone indicated when the action should start. Prolongation of movement duration may have been determined by the necessity to accommodate the processing required to integrate these instructions.

This is further confirmed by the finding that time of maximum grip aperture was delayed for the ‘constrained’ condition in comparison to the ‘voluntary’ condition. Because participants were instructed to start the action at the presentation of the second tone, it is plausible that in the ‘constrained’ condition, after movement onset (that was indeed anticipated in comparison to the ‘voluntary’ condition), they slowed down to recover and implement the instruction about which object to grasp (‘what’ component).

4.2. The www model

As previously reported, *what*, *whether*, and *when* decision components can be dissociated at a functional level (Brass & Haggard, 2008; Haggard, 2008). Furthermore, while there are still some inconsistencies, there is evidence that these components may be partly dissociable at a neuroanatomical level (Kriehoff et al., 2011). In the following, the specific effects of *what*, *whether*, and *when* decision components on kinematics are discussed in relation to behavioural and neuroimaging evidence.

4.2.1 What component: deciding what to do

The ‘*what*’ component reflects the decision of which action to perform and is commonly tested in free choice paradigms in which participants can freely choose between different action alternatives (e.g., Lau, Rogers, Haggard, & Passingham, 2004; Muller, Von Mühlenen, & Geyer, 2007). For example, in a functional MRI (fMRI) experiment, Lau et al. (2004) compared a free selection condition in which participants selected a target with a specified condition in which they

had to move the cursor to a specified target. The comparison of freely selected versus specified actions revealed activations in different parts of the fronto-median cortex including the anterior cingulate cortex, the presupplementary motor area (preSMA), and the parietal cortex. Other studies, using similar paradigms, report activations in the anterior cingulate cortex and the pre-SMA, suggesting that these areas might be specifically involved in the intentional selection between different response alternatives (e.g., Muller et al., 2007; Kriehoff, Brass, Prinz, & Waszak, 2009).

In the present study, the *what* decision component was operationalized as a choice between a small and large target object. We found that constraining this choice (Experiment 2) selectively affected two key measures, namely movement time and time to maximum grip aperture. In particular, as reported above, movement time was longer and maximum grip aperture was reached later in time for the ‘voluntary’ compared to the ‘what constrained’ condition. We suggest that this pattern might reflect the intentional processing of response alternatives in the ‘voluntary’ condition. To elaborate, in the ‘what constrained’ condition, participants were told which action to make prior to the beginning of each trial. In the ‘voluntary’ condition, by contrast, there were no instructions about which action to make and participants freely selected one action amongst two alternatives (grasp the large target vs. grasp the small target). To the extent that for the ‘voluntary’ condition both alternatives were simultaneously represented at a motor level (Cisek & Kalaska, 2005; Klein-Flügge & Bestmann, 2012), this could explain the increase in movement duration.

In contrast to movement duration, time to maximum grip aperture has been proposed to reflect control during movement execution rather than advanced planning (Glover, 2004). That time to maximum grip aperture was also delayed might indicate that control processes for voluntary reach-to-grasp actions were slowed down.

4.2.2 *Whether component: deciding whether to do it*

The *whether* decision component has been proposed to have both an early motivational component (early *whether* decisions) and a final predictive check (late *whether* decisions), related to

the possibility to cancel an already selected action (Haggard, 2008). One possibility to investigate this latter inhibitory component is to ask participants to first prepare an action and then to decide for themselves whether to perform or inhibit it. Following this approach, Brass and Haggard (2007) instructed participants, in an fMRI study, to prepare and perform simple key pressers at a time of their own choosing, but to withhold the action at the last possible moment on some trials. The dorsal frontomedian cortex, an area located dorsally to the anterior cingulate cortex associated with *what* decisions, was activated in veto trials more than in trials in which participants made actions. Similarly, Kühn and Brass (2009) found differential activation within the dorsal frontomedian cortex when contrasting trials with a voluntary decision to inhibit with trials with a voluntary decision to proceed with the prepared action. Interestingly, the analyses revealed a significant correlation between each participant's percentage of inhibited trials and inhibition-related activity in the dorsal frontomedian cortex, further supporting the view that this area may act as a 'brake' on motor output.

At a behavioural level, responses which depend on late *whether* decisions are characterized by longer delays (600 ms) as compared to instructed responses (Filevich, Kühn, & Haggard, 2013). This has been taken to suggest that the free decision to respond or transiently inhibit a response involved a time-consuming cognitive process that may delay movement preparation. Our findings of longer movement duration for voluntary compared to whether instructed decision add to this evidence, suggesting that not only the initiation of a response, but also the programming of movement time may be influenced by late *whether* decision components. In particular, it could be hypothesized that longer movement durations for voluntary compared to 'whether constrained' movements reflect the preactivation of a voluntary 'neural brake' mechanisms, which, without stopping the movement, slows down its execution so to enable a quicker late *whether* decision when it is needed (Aron, 2011).

4.2.3 When component: deciding when to do it

Whereas the timing of stimulus-driven actions is determined by an external stimulus, voluntary actions often depend on a *when* decision component related to when to perform the action. Using free choice paradigms, several studies have compared brain activity between self-paced conditions, in which the participant themselves decides when to make an action, and externally triggered conditions, in which the participant makes a similar action in response to a stimulus. Activity within the dorsolateral prefrontal cortex and the frontomedian cortex has been identified by this comparison (e.g., Deiber, Honda, Ibanez, Sadato, & Hallett, 1999; Kriehoff et al., 2009; Soon, Brass, Heinze, & Haynes, 2008). Recent attempts to disentangle the *what* and *when* components of voluntary actions suggest that whereas the preSMA may be specifically associated with the free choice of the executed movements (*what*), free timing of movement execution (*when*) may rely crucially on the SMA, the insula, and the bilateral anterior putamen and globus pallidus, which together with the preSMA motor area are known as the medial premotor system (Hoffstaedter, Grefkes, Zilles, & Eickhoff, 2013).

Experiment 2 suggests that at a kinematic level, the influence of the *when* decision component was confined to the time of maximum grip aperture. This was reached earlier for ‘when constrained’ actions in comparison to ‘voluntary’ actions, indicating that voluntary selection of the timing of an action may influence approach parameters.

Interestingly, despite movement onset was generally shorter for ‘when constrained’ action, the *when* decision component did not influence the overall duration of the action. This suggests that the *internal selection* of the action (*what* decision component), but not the *internal timing* of the action (*when* decision component), may impact on advanced movement planning.

5. Conclusions

Voluntary actions involve several decisions components that are absent from stimulus-driven actions: decisions about what to do, decisions about whether to do it, and decisions of when

to do it (Brass & Haggard, 2008). Our results provide the first demonstration of how these decision components influence different aspects of the reach-to-grasp movement in a selective fashion. These findings add to current models of volition suggesting that (i) voluntary and stimulus-driven control are differently implemented at a motor level; (ii) voluntary motor control results from an interplay of subfunctions related to the decision of *what* action execute, *when* to execute an action, and *whether* to execute any action or not.

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References

- Ansuini, C., Giosa, L., Turella, L., Altoè, G., & Castiello, U. (2008). An object for an action, the same object for other actions: effects on hand shaping. *Experimental Brain Research*, 185, 111-119.
- Ansuini, C., Santello, M., Massaccesi, S., & Castiello, U. (2006). Effects of end-goal on hand shaping. *Journal of Neurophysiology*, 95, 2456–2465.
- Aron, A. R. (2011). From reactive to proactive and selective control: developing a richer model for stopping inappropriate responses. *Biological Psychiatry*, 69, 55-68.
- Astor-Jack, T., & Haggard, P. (2005). Intention and reactivity. In Humphreys, G. W., & Riddoch, M. J. (Eds.), *Attention in action: advances from cognitive neuroscience* (pp. 109-131). New York: Psychology Press.
- Becchio, C., Sartori, L., Bulgheroni, M., & Castiello, U. (2008a). The case of Dr. Jekyll and Mr. Hyde: a kinematic study on social intention. *Consciousness and cognition*, 17, 557-564.
- Becchio, C., Sartori, L., Bulgheroni, M., & Castiello, U. (2008b). Both your intention and mine are reflected in the kinematics of my reach to grasp movement. *Cognition*, 106, 894-912.
- Brass, M., & Haggard, P. (2007). To do or not to do: the neural signature of self-control. *Journal of Neuroscience*, 27, 9141–9145.
- Brass, M., & Haggard, P. (2008). The what, when, whether of intentional action. *Neuroscientist*, 14, 319–325.
- Cisek, P. (2006). Integrated neural processes for defining potential actions and deciding between them: A computational model. *Journal of Neuroscience*, 26, 9761-9770.
- Cisek, P. (2007). Cortical mechanisms of action selection: the affordance competition hypothesis. *Philosophical Transactions of the Royal Society B*, 362, 1585-1599.
- Cisek, P. (2012). Making decisions through a distributed consensus. *Current Opinion in Neurobiology*, 22, 927-936.
- Cisek, P., & Kalaska, J. F. (2005). Neural correlates of reaching decisions in dorsal premotor cortex: specification of multiple direction choices and final selection of action. *Neuron*, 45, 801-814.
- Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*, 33, 269-298.
- 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, 373–385.

- 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. *Journal of Neurophysiology*, 81, 3065–3077.
- Doya, K., & Shalden, M. N. (2012). Decision making. *Current Opinion in Neurobiology*, 22, 911-913.
- Donders, F. C. (1868). Over de snelheid van psychische processen. *Onderzoekingen gedaan in het Physiologisch Laboratorium der Utrechtsche Hoogeschool, 1868-1869, Tweede reeks*, II, 92-120.
- Filevich E., Kühn S., & Haggard P. (2013). There is no free won't. Antecedent brain activity predicts decision to inhibit. *PLoS ONE*, 8, e53053.
- Friston, K. (2008). Hierarchical models in the brain. *PLoS Computational Biology*, 4, e1000211.
- Gentilucci, M., Castiello, U., Corradini, M. L., Scarpa, M., Umiltà, C., & Rizzolatti, G. (1991). Influence of different types of grasping on the transport component of prehension movements. *Neuropsychologia*, 5, 361–378.
- Georgiou, J., Becchio, C., Glover, S., & Castiello, U. (2007). Different action patterns for cooperative and competitive behaviour. *Cognition*, 102, 415-433.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, 27, 3-24; discussion 24-78.
- Jakobson, L. S., & Goodale, M. A. (1991). Factors affecting higher-order movement planning: a kinematic analysis of human prehension, *Experimental Brain Research*, 86, 199-208.
- Jenkins, I. H., Jahanshani, M., Jueptner, M., Passingham, R. E., & Brooks, D. J. (2000). Self-initiated versus externally triggered movements II. The effect of movement predictability on regional cerebral flow. *Brain*, 123, 1216-1228.
- Haggard, P. (2008). Human volition: towards a neuroscience of will. *Nature Reviews Neuroscience*, 9, 934-46.
- Hart, S. G. (1986). Theory and measurement of human workload. In J. Zeidner (Eds.), *Human productivity enhancement: Training and human factors in system design* (Vol. 1., pp. 396-456). New York: Praeger.
- Hughes, G., Schütz-Bosbach, S., & Waszak, F. (2011). One action system or two? evidence for common central preparatory mechanisms in voluntary and stimulus-driven actions. *Journal of Neuroscience*, 31, 16692–16699.
- Hoffstaedter, F., Grefkes, C., Zilles, K., & Eickhoff, S. B. (2013). The “what” and “when” of self-initiated movements. *Cerebral Cortex*, 23, 520–530.

- Klein-Flügge, & M. C., Bestmann, S. (2012). Time-dependent changes in human cortico-spinal excitability reveal value-based competition for action during decision processing. *Journal of Neuroscience*, 32, 8373-82.
- Krieghoff, V., Brass, M., Prinz, W., & Waszak, F. (2009). Dissociating what and when of intentional actions. *Frontiers in Human Neuroscience*, 3, 1–10.
- Krieghoff, V., Waszak, F., Prinz, W., & Brass, M. (2011). Neural and behavioral correlates of intentional actions. *Neuropsychologia*, 49, 767 – 776.
- Kubaneck, J., & Kaplan, D. M. (2012). Evidence for a decision variable in the human motor system *Journal of Neuroscience*, 32, 8110-8111.
- Kuhn, S., & Brass, M. (2009) When doing nothing is an option: the neural correlates of deciding whether to act or not. *Neuroimage*, 46, 1187–1193.
- Lau, H. C., Rogers, R. D., Haggard, P., & Passingham, R. E. (2004). Attention to intention. *Science*, 303, 1208-1210.
- Meulenbroek, R. G., Van Galen, G. P., Hulstijn, M., Hulstijn, W., & Bloemsaat, G. (2004). Muscular co-contraction covaries with task load to control the flow of motion in fine motor tasks. *Biological Psychology*, 68, 331-352.
- Müller, H. J., Von Mühlenen, A., & Geyer, T. (2007). Top-down inhibition of distractors in parallel visual search. *Perception & Psychophysics*, 69, 1373-1388.
- Obhi, S. S., & Haggard, P. (2004). Internally Generated and Externally Triggered Actions are physically distinct and independently controlled. *Experimental Brain Research*, 156, 518-523.
- Obhi, S. S., Matkovich, S., & Gilbert, S. J. (2008). Modification of planned actions. *Experimental Brain Research*, 192, 265-274.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, 9, 97-113.
- Paulignan, Y., MacKenzie, C., Marteniuk, R., & Jeannerod, M. (1990). The coupling of arm and finger movements during prehension. *Experimental Brain Research*, 79, 431-435.
- Sartori, L., Becchio, C., Bulgheroni, M., & Castiello U. (2009). Modulation of the action control system by social intention: unexpected social requests override preplanned action. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 1490-1500.
- Sartori, L, Becchio, C, & Castiello, U. (2011). Cues to intention: The role of movement information. *Cognition*, 119, 242-252.
- Soon, C., Brass, M., Heinze, H., & Haynes, J. (2008). Unconscious determinants of free decisions in the human brain. *Nature Neuroscience*, 11, 543–545.

Schüür, F., & Haggard, P. (2011). What are self-generated actions? *Consciousness and Cognition*, 20, 1697–1704.

Selen, L. P., Shadlen, M. N., & Wolpert, D.M. (2012). Deliberation in the motor system: reflex gains track evolving evidence leading to a decision. *Journal of Neuroscience*, 32, 2276–2286.

Shalden, M. N., Kiani, R., Hanks, T. D., & Churchland, A. K. (2008). Neurobiology of decision making: an intentional framework. In Engel, C., & Singer, W. (Eds.), *Better Than Conscious? Decision Making, the Human Mind, and Implications for Institutions* (pp. 71-101). Cambridge: MIT Press.

Waszak, F., Wascher, E., Keller, P., Koch, I. Aschersleben, G. Rosenbaum, D. A., & Prinz, W. (2005). Intention-based and stimulus-based mechanism in action selection. *Experimental Brain Research*, 162, 346-356.

Wing, A. M., Turton, A., & Fraser, C. (1986). Grasp size and accuracy of approach in reaching. *Journal of Motor Behavior*, 18, 245-260.

Figures

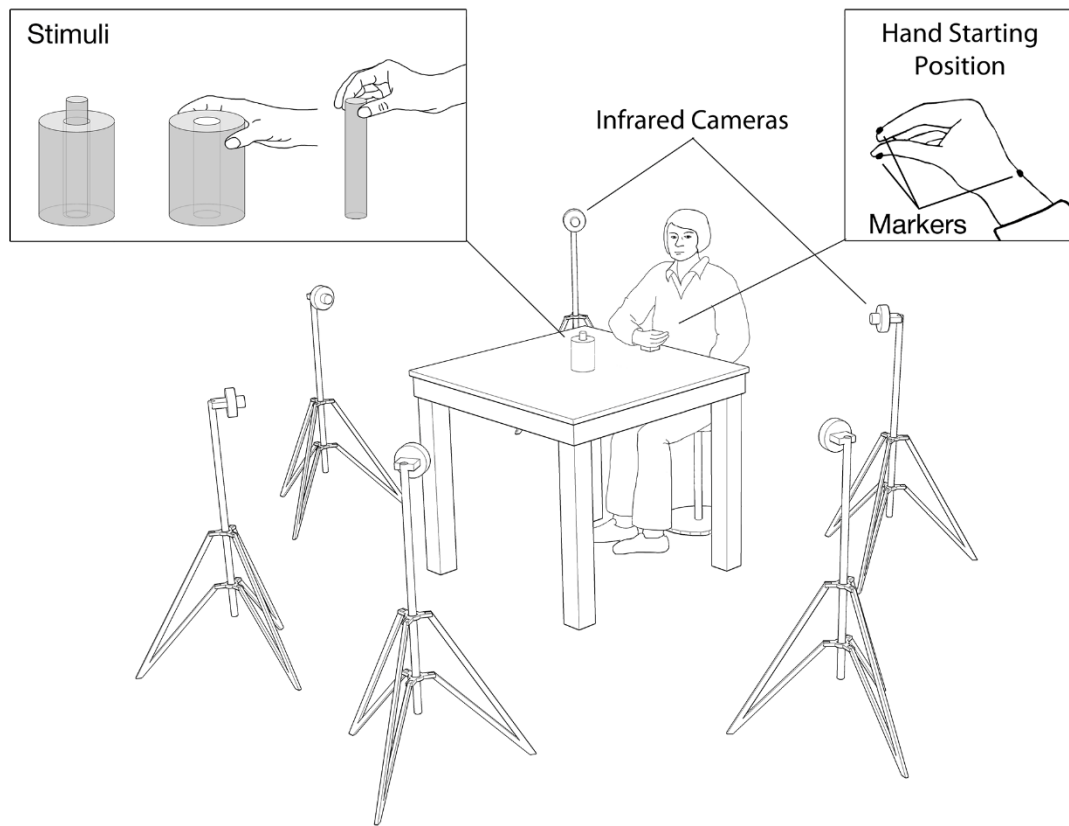


Figure 1. Graphical representation of the experimental set up, the objects used as targets, the hand starting position adopted by each subjects at the beginning of each trials and the markers' position. Note that the large and the small cylinders were grasped with a power and a precision grip, respectively.

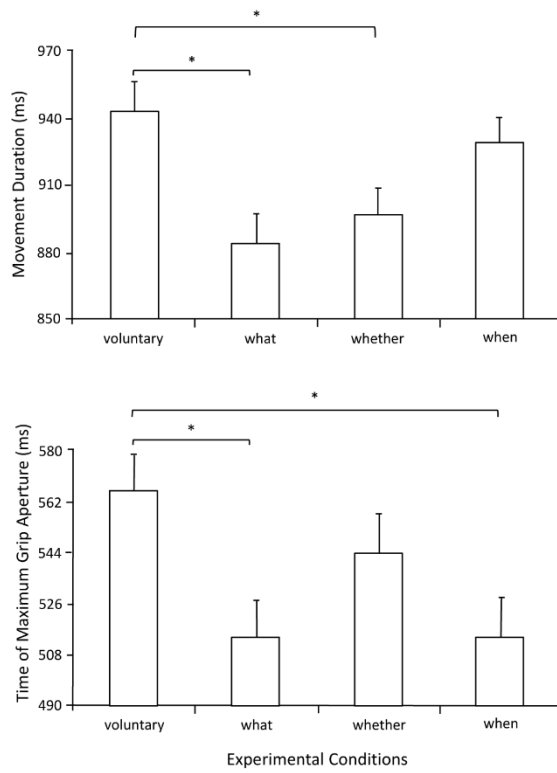


Figure 2. Movement duration and the time to maximum grip aperture for the different experimental conditions in Experiment 2. Bars represent the standard error of means.