Motor command inhibition and the representation of response mode during motor imagery

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ABSTRACT

Research on motor imagery proposes that overt actions during motor imagery can be avoided by proactively signaling subthreshold motor commands to the effectors and by invoking motor-command inhibition. A recent study by Rieger, Dahm, and Koch (2017) found evidence in support of motor command inhibition, which indicates that MI cannot be completed on the sole basis of subthreshold motor commands. However, during motor imagery, participants know in advance when a covert response is to be made and it is thus surprising such additional motor-command inhibition is needed. Accordingly, the present study tested whether the demand to perform an action covertly can be proactively integrated by investigating the formation of task-specific action rules during motor imagery. These task-specific action rules relate the decision rules of a task to the mode in which these rules need to be applied (e.g., if smaller than 5, press the left key *covertly*). To this end, an experiment was designed in which participants had to switch between two numerical judgement tasks and two response modes: covert responding and overt responding. First, we observed markers of motor command inhibition and replicated the findings of Rieger and colleagues. Second, we observed evidence suggesting that task-specific action rules are created for the overt response mode (e.g., if smaller than 5, *press the left key*). In contrast, for the covert response mode, no task-specific action rules are formed and decision rules do not include mode-specific information (e.g., if smaller than 5, left).
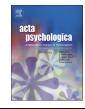
1. Introduction

Motor imagery (MI) refers to a dynamic state during which the representation of a given motor act is internally rehearsed within working memory without any overt movement (Decety & Grèzes, 1999, p. 177; see also Guillot & Collet, 2010; Moran, Guillot, MacIntyre, & Collet, 2012). MI-based techniques are widely used for optimizing a variety of complex skills such as in athletics (see Weinberg, 2008, for a review), typing (Nyberg, Eriksson, Larsson, & Marklund, 2006), playing music (e.g., Highben & Palmer, 2004; Lim & Lippman, 1991), or even surgical interventions (e.g., Rogers, 2006). A key proposal of MI is the Motor Simulation Theory (MST) developed by Jeannerod (1994, 2001, 2006). MST is based on the assumption that MI includes motor representations, which are also involved in the preparation and initiation of actual movements (Jeannerod, 1994). This stance is evidenced by a substantial body of neuro-physiological research indicating that the neural circuitry underlying MI partially overlaps with the neural circuitry underlying the overt execution of actions (cf. Burianová et al., 2013; Kraeutner, Gionfriddo, Bardouille, & Boe, 2014). In addition, mental-

chronometry procedures have repeatedly demonstrated a functional similarity between covert and overt action, namely the time needed to perform a particular action covertly co-varies with the time needed to execute an action overtly (i.e., isochrony, see Guillot, Hoyek, Louis, & Collet, 2012, McAvinue & Robertson, 2008, for reviews). For instance, Decety, Jeannerod, and Prablanc (1989) observed that increasing the length of a particular walking distance not only increases the actual walking time but also the imagined walking time.

Following MST, motor representations common to overt and covert action are activated through a simulation mechanism during MI (Jeannerod, 2001, 2006). Yet, whereas MI relies on the same representations as the overt action it simulates, the overt action (i.e., actual execution) itself is absent (Jeannerod, 2004, 2006). MI thus constitutes a paradox in which motor representations are activated, on the one hand, and overt movements are avoided, on the other hand (see Guillot, Di Rienzo, MacIntyre, Moran, & Collet, 2012, p. 2; Jeannerod, 2001, p. S106 for a similar argument). Jeannerod (2001) proposed two mechanisms through which overt actions are avoided. First, motor activation during MI is subliminal, such that it is insufficient to instantiate

overt action. Second, motor output during MI is blocked by an inhibitory process, which is generated in parallel with motor activation. Similarly, Guillot, Hoyek, et al. (2012) provided a review on research focusing on motor inhibition during MI and proposed that overt actions during MI are avoided in three complementary ways: (a) the demand to perform covert responses is part of the imagery experience and integrated within the construction of the mental representation of the imagined action, such that only *subthreshold motor commands* are signaled to the effectors; (b) motor commands specific for the effector used in the imagined condition are weakened by inhibitory cerebral regions, possibly complemented with cerebellar and spinal inhibitory influences (i.e. *effector-specific motor-command inhibition*); and (c) all motor activity is inhibited (*global motor-command inhibition*).

As pointed by Guillot, Hoyek, et al. (2012, p. 8), motor-command inhibition during MI shows parallels with a well-documented phenomenon in cognitive psychology, namely response inhibition in which participants are required to withhold an overt response when a specific signal is presented (see Verbruggen & Logan, 2008, 2009 for reviews). A common finding in research on response inhibition is that trials following a trial on which a response was inhibited are responded to much more slowly, which has been attributed to residual inhibitory processing (e.g., Rieger & Gauggel, 1999; Verbruggen, Logan, Liefooghe, & Vandierendonck, 2008). Based on this type of findings, Rieger, Dahm, and Koch (2017) investigated the processes underlying MI by comparing aftereffects of overt and covert responding (i.e., MI). To this end, they developed a novel response-mode switching paradigm. A computer display presented four horizontally aligned empty circles, which corresponded with four horizontally aligned response keys. When a circle was filled, participants had to press the corresponding response key. For the two leftwards circles, the left hand had to be used. For the two rightwards circles, the right hand had to be used. Depending on the color of the filled circle, participants responded to a trial either overtly or covertly. More precisely, participants had to release a rest-key and press the corresponding response key overtly or covertly before returning to the rest key. Such procedure provides two dependent measures, which are common to overt and covert responding: Release Times (the time between stimulus onset and releasing the rest-key) and Inter Rest-Key Intervals (the time interval between releasing the rest-key and re-entering the rest-key). In the condition of interest, the mode repeated or switched on a trial-by-trial basis and four trial sequences were created: C (covert trial n − 1)–O (overt trial n) sequences; O-O sequences; O-C sequences and C-C sequences. Release Times were longer for C-O sequences than for O-O sequences. Switching from the covert to the overt mode thus elicited a mode switch cost. The difference between C-C and O-C sequences was not significant. Inter Rest-Key Intervals were longer for C-C sequences compared to O-C sequences. A mode switch benefit was thus observed. Inter Rest-Key Intervals did not differ significantly between O-O and C-O sequences. Rieger et al. (2017) concluded that the aftereffects of MI they observed provided evidence for global motor-command inhibition. This inhibition persists over time and affects performance on trial n. Avoiding an overt response on trial n − 1 impairs the motor commands involved in executing an overt response on trial n, but also the motor commands involved in releasing and re-entering the rest-key. Additional analyses were also conducted in which the repetition of specific hand movements across two trials was taken into account (i.e., hand repetition vs. hand alternation). Hand repetitions were slower than hand alternations in the C-C and C-O sequences, whereas the reverse pattern was observed for the O-O sequences. Rieger et al. (2017) interpreted this pattern as evidence for the hypothesis that MI is also associated with effector-specific motor-command inhibition, which hampers the repetition of the same effector across two trials. Interestingly, Rieger et al. (2017) also compared complete repetitions (i.e., same hand, same stimulus) with partial repetitions (i.e., same hand, different stimulus), but did not observe differences between both, which led to the conclusion that MI does not involve action-specific motor-command inhibition.

The findings of Rieger et al. (2017) stress the importance of global and effector-specific motor command inhibition during MI and the specific pattern of after-effects they observed is difficult to reconcile with the idea that MI is solely based on subthreshold commands, without invoking additional motor-command inhibition. However, this does not exclude that motor commands during MI may be weaker compared to actual response execution, nor that the demand to perform a task covertly is somehow proactively integrated with the other features of task. As pointed out by Guillot, Di Rienzo, et al. (2012, p. 8), when participants engage in MI they know *in advance* that only a covert movement is required and it would be puzzling that overt movements during MI can only be avoided through motor command inhibition. In analogy, research on response inhibition recently demonstrated that response inhibition also depends on preparatory processes, which proactively adjust the necessary attentional and response parameters in view of the future requirement to inhibit a response when needed (Elchlepp, Lavric, Chambers, & Verbruggen, 2016; Verbruggen, Stevens, & Chambers, 2014). This state of affairs raises the question to which extent the demand to respond covertly can be integrated proactively with the other features of an imagined movement, when signaled that MI ensues. In the present study, we tested this issue by investigating whether task-specific action rules are created during MI. These rules integrate the decision rules of a particular task (e.g., odd-left, even-right) with the parameters specifying the response modality in which these decisions rules need to be applied (e.g., saying the word left, pressing a left key; Philipp & Koch, 2010). The central question was if such task-specific action rules are created when signaled that a task needs to be performed covertly (i.e., MI), such as 'if smaller than 5, press the left key *covertly*'. To this end, the procedure of Rieger et al. (2017) was extended to also incorporate task switches besides response-mode switches.

Task switching has been widely used in order to investigate how different task parameters are represented and configured (see Kiesel et al., 2010; Monsell, 2003; Vandierendonck, Liefooghe, & Verbruggen, 2010, for reviews). A core observation in task switching is the task-switch cost, which manifests itself as higher reaction times and error rates when the task switches compared with repeating the same task as in trial n − 1. The switch cost offers a marker of the processes involved in configuring the cognitive system towards a new task, which prepare for that task (e.g., Rogers & Monsell, 1995) and shield the cognitive system from proactive interference emanating from previously executed tasks (e.g., Dreisbach & Haider, 2009; see also Vandierendonck et al., 2010, for an extensive review of the interplay between preparation and interference in task switching). The task-switch cost has been frequently used as a marker to measure how different task parameters are organized when performing a task (e.g., Allport, Styles, & Hsieh, 1994; Hübner, Futterer, & Steinhauser, 2001; Kleinsorge & Heuer, 1999; Philipp & Koch, 2010; Vandierendonck, Christiaens, & Liefooghe, 2008). These parameters can be thought of as cognitive representations of the different components of a task, such as the goal of that task, the stimulus-response categorization rules needed to achieve the task goal, the response modality, the relevant stimulus dimension, and so on. Previous research demonstrated that in some cases task parameters are integrated into a single representation underlying task performance, which is commonly labelled the *task-set* (Rogers & Monsell, 1995). Evidence for this hypothesis comes from task-switching studies in which not only tasks can repeat or switch, but also the relevant stimulus dimension (Vandierendonck et al., 2008) or the response modality (Hübner et al., 2001; Kleinsorge & Heuer, 1999; Philipp & Koch, 2010). Philipp and Koch (2010) used a task-switching design in which participants had to switch between two tasks (e.g., parity and magnitude judgments) and two overt response modalities (verbal, manual). They observed that the cost of switching both the response modality and the task at the same time was almost similar to the cost of changing the response modality (modality switching) or the task (task switching) separately. Such under-additive switch-pattern (i.e., cost of changing