Motor Imagery entails Task-set Inhibition

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Abstract

Motor imagery requires the covert execution of a movement without any overt motor output. Previous studies indicated that motor imagery results in the prolonged inhibition of motor commands. In the present study, we investigated whether motor imagery also leads to the inhibition of more abstract task representations. To do so, we investigated the effect of motor imagery on $n - 2$ repetition costs, which offer an index of the extent to which task representations are inhibited. Participants switched among three tasks and among two response modes: overt and covert responding (i.e., motor imagery). $N - 2$ repetition costs were present when the current trial required an overt response but absent when the current trial required a covert response. Furthermore, $n - 2$ repetition costs were more pronounced when trial $n - 1$ required a covert response rather than an overt response. This pattern of results suggests that motor imagery also leads to the inhibition of abstract task representations. We discuss our findings in view of current conceptualizations of motor imagery and argue that the inhibitory mechanism entailed by motor imagery targets more than motor commands alone. Finally, we also relate our findings to the mechanisms underlying the inhibition of task representations.

Keywords: Task switching; motor imagery; inhibition

1. Introduction

Motor Imagery (MI) can be defined as a dynamic state of internally rehearsing the mental representation of a motor act within working memory without actually performing this motor act (Decety, 1996). Although MI is widely used as a tool for training and optimizing motor skills of various kinds (e.g., Dickstein & Deutsch, 2007; Schuster et al., 2011), the nature of its underlying cognitive processes still remains an open question (see O'Shea & Moran, 2017 for a review). A common assumption of the so-called Motor Simulation Theory (Jeannerod, 1994, 2001, 2006) is that MI includes motor representations that are also involved in the preparation and initiation of overt movements. This supposition is supported by the notion that MI and overt movements partially share neural circuits (cf. Burianová et al., 2013; Kraeutner, Gionfriddo, Bardouille, & Boe, 2014). However, due to the shared nature of imagined and actual actions, MI must involve mechanisms that prevent an overt movement when the mental representation of that action is activated. Two mechanisms have been proposed, which can operate in conjunction to suppress overt movements during MI (e.g., Guillot, Di Rienzo, MacIntyre, Moran, & Collet, 2012; Jeannerod, 2001, 2006; Ridderinkhof, van den Wildenberg, & Brass, 2014; Stinear, 2010). On the one hand, because people know in advance that they will need to perform an action covertly, this can be prepared for and only subthreshold signals are sent to the motor system so that overt movements cannot be triggered. On the other hand, the neural activation caused by MI may be blocked by an inhibitory mechanism, which prevents overt action. This mechanism can either inhibit all motor commands or, alternatively, it can target specific effectors or actions (Guillot et al., 2012).

In recent years behavioral research took interest in the nature of the inhibitory mechanism, which supposedly blocks overt movement during MI (e.g. Rieger, Dahm, & Koch, 2017; Scheil & Liefoghe, 2018; O'Shea & Moran, 2018). For instance, Rieger, Dahm, and Koch (2017) investigated the nature of this inhibitory mechanism by introducing the response-mode switching paradigm and measuring aftereffects of MI. 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 permits to estimate the time needed to perform a response covertly by measuring the time needed to release and re-enter the rest-key in relation to the stimulus onset. 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. Rieger and colleagues (2017) observed a response-mode switch cost when contrasting C-O sequences and O-O sequences. In contrast, a response-mode switch benefit was observed when comparing C-C sequences with O-C sequences. Rieger et al. (2017) interpreted these aftereffects by suggesting that neural activation in MI is blocked by global motor-command inhibition. When responding covertly on trial $n - 1$, all motor commands are inhibited. This inhibition persists over time and affects performance on trial n . This impairs the execution of an overt response on trial n , but also the motor commands involved in releasing and re-entering the rest-key.

Rieger et al. (2017) also conducted additional analyses 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 also leads to inhibition of effector-specific motor command, which hampers the repetition of the same effector across two trials. Interestingly, Rieger and colleagues (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.

Scheil and Liefoghe (2018) elaborated the procedure of Rieger et al. (2017) by using two tasks in the response-mode switching paradigm, such that participants not only switched between two response modes (i.e., covert, overt), but also between two tasks (i.e., task-switching). In line with Rieger et al. (2017), they observed aftereffects suggesting that all motor commands are

inhibited following MI. In contrast, Scheil and Liefoghe (2018) also obtained evidence indicating that the inhibitory mechanism associated with MI can also target specific actions (cfr. Rieger et al., 2017). In addition, these authors observed that the costs of switching the task and switching the response mode were additive (i.e., cost of changing task and response mode = cost of changing task + cost changing response mode). Based on previous work by Philipp and Koch (2010), Scheil and Liefoghe (2018) proposed that when preparing to perform a task covertly, participants do not create task-specific action rules, which incorporate both the response mode and the decision rules of that task (e.g., if larger than 5, press left *covertly*; if smaller than 5, press right *covertly*).

The inhibitory mechanism involved in MI thus can either lead to the inhibition of all motor commands (Rieger et al., 2017; Scheil & Liefoghe, 2018), but also target specific effectors (Rieger et al., 2017) or actions (Scheil & Liefoghe, 2019). In the present study, we go one step further in the investigation of this inhibitory mechanism, by testing whether it also targets more abstract task-sets, which underlie the execution of an action or a task (cf. Kiesel et al., 2010). Such task-set includes representations of relevant structural task elements (e.g., contextual cues, stimuli, and responses) and how these are interrelated (e.g., stimulus-response mappings). Previous research demonstrated that such task-sets can become inhibited as a whole (see Koch, Gade, Schuch, & Philipp, 2010; Koch, Poljac, Müller, & Kiesel, 2018; Vandierendonck, Liefoghe, & Verbruggen, 2010, for reviews). Such task-set inhibition is measured by using the $n - 2$ repetition cost. This cost is measured in task-switching procedures using at least three tasks (e.g., Mayr & Keele, 2000), for instance, tasks A, B, and C. Typically, reaction times (and sometimes error rates) are higher when participants switch from one task to another one and then back to the task that was relevant in trial $n - 2$ (sequences of type ABA) compared to two consecutive switches to another task each (sequences of type CBA). This effect is commonly explained by inhibitory processes, which reduce interference of task-sets that are currently irrelevant. In each trial, inhibition is released that persists for a certain time and decreases again. If the inhibited task-set has to be performed soon (that is, two trials later in ABA sequences), the task-set is still in a partially inhibited state, making it more difficult to activate it again. In CBA sequences, on the contrary, the last encounter with task-set A lies at least three trials back,

minimizing the amount of inhibition still present. The $n - 2$ repetition cost is a robust finding (see Koch et al., 2010 for a review) and offers an index of the equilibrium between the inhibition and activation of task-sets (see Grange, Juvina, & Houghton, 2013). An increased $n - 2$ repetition cost thus indicates that task-set inhibition outweighs task-set activation, but the absence of $n - 2$ repetition costs does not rule out the presence of task-set inhibition. It merely indicates that task-set inhibition and task-set activation are in balance.

Various hypotheses have been put forward about the specific aspects of how task-sets are targeted by inhibition. Some results favor response-related inhibition (e.g., Schuch & Koch, 2003), others are in line with inhibition targeting cue-based preparation (e.g., Scheil, 2016; Scheil & Kleinsorge, 2014). Another explanation is that inhibition targets the aspect of the task-set that bears the highest conflict potential (Houghton, Pritchard, & Grange, 2009). A distinction between these assumptions is complicated by the fact that $n - 2$ repetition costs as a proxy of inhibition represent a net measure of inhibition and activation processes over a series of three trials. As a consequence, a differentiation between aspects that trigger inhibition in the context of task switching on the one hand and the target of inhibition on the other hand may be blurred. In addition, it makes it difficult to distinguish whether brain areas correlated with $n - 2$ repetition costs can be supposed to play a role in releasing inhibition or in overcoming it (Dreher & Berman, 2002). However, despite these research questions that are still unacknowledged, the common assumption prevails that $n - 2$ repetition costs are due to inhibition of abstract task-set representations, with the aim to reduce interference among tasks (cf. Koch et al., 2010).

In order to investigate whether the inhibitory mechanism, which is associated with MI, also results in the inhibition of task-sets, we investigated whether $n - 2$ repetition costs, measured on a trial n , are modulated by the demand to perform a task overtly or covertly on trial $n-1$ (i.e., MI). The rationale of this approach is that if MI also leads to task-set inhibition, then the size of $n - 2$ repetition costs should be modulated when incorporating MI in a task-switching procedure including three tasks. Following the lateral inhibition account of $n - 2$ repetition costs, this cost is due to an inhibitory mechanism that can be characterized as a by-product of activating the following task in case of a task

switch (Gade & Koch, 2005; Philipp & Koch, 2006). Specifically, it is assumed that inhibition of the task-set that was relevant in trial $n - 2$ is linked to the preparation of the task that has to be performed in trial $n - 1$ (because this is the timeframe when a task repetition, in which case inhibition would not make any sense, can be excluded). This assumption was, for example, corroborated by the finding of Scheil and Kleinsorge (2014) that $n - 2$ repetition costs depend on the preparation time in trial $n - 1$. Hence, if participants prepare for a covert trial during the preparation interval of trial $n - 1$, by invoking an inhibitory mechanism, which also targets task-sets, then the demand to perform a task covertly on trial $n-1$ should amplify the task-set inhibition that causes the $n - 2$ repetition cost and thus larger $n - 2$ repetition costs are predicted compared to XXX. To test this, we used the experimental setting of Scheil and Liefoghe (2018) in a slightly adapted version with three tasks and without task repetitions. In half of the trials, participants had to respond by pressing a key, whereas in the other half, the movement had to be executed covertly via MI. Response mode was cued by different colors of the task cue. Participants had to press the spacebar at the beginning of each trial (overt and covert). This was done in order to be able to measure behavioral data in case of imagined movements. In case of an overt trial, participants had to release the spacebar, press the response key, and press the spacebar again immediately afterwards. In case of a covert trial, participants had to release the spacebar, imagine the movement to the response key, and press the spacebar again immediately afterwards (see also Rieger et al., 2017; Scheil & Liefoghe, 2018; Theeuwes, Liefoghe, De Schryver, & De Houwer, 2018, for a similar procedure).

2. Material and Methods

2.1 Participants

An original sample of 36 right-handed volunteers participated (7 males, mean age = 24.19 years). Six participants had to be excluded due to a mean error rate of $> 38\%$ (mainly due to participants failing to get used to the trial procedure, dropping the spacebar too early or pressing it too late), while the remaining participants had a mean error rate of 14% (range: 1%-30%). The cut-off was set at 33%. Please note that these error rates refer not only to task or response errors (pressing the wrong key) but to the total number of incorrect trials, also including errors in the trial procedure

(like incorrectly pressing and lifting the spacebar). The final sample consisted of 5 men and 25 women with a mean age of 24.06 years (range: 19-29). All participants had normal or corrected-to-normal vision. All of them signed informed consent approved by the Ethical Committee of IfADo.

2.2 Stimuli, tasks, and apparatus

Stimuli consisted of two different shapes (x and +) presented with either a solid or a dashed line and with a size of either 3 cm x 3 cm or 6 cm x 6 cm. Task cues consisted of a diamond, square, or triangle surrounding the position of the imperative stimulus with a size of about 7 cm x 7 cm. Participants switched among three perceptual decision tasks in which they had to judge the stimuli regarding their size (large vs. small, indicated by the diamond), lining (solid or dashed, indicated by the square), or their shape (x or +, indicated by the triangle). The covert and overt mode was cued by the color of the cues. Two colors per mode were used, without color repetitions. For half of the participants, the demand to respond overtly was indicated by two warm colors (orange and pink), whereas covert responses were cued by two cold colors (blue and green). For the other half of the sample, the colors were reversed. All tasks occurred with equal frequency. All variables (tasks, task sequence, mode, mode transition, responses, and colors) were pseudo-randomized across four experimental subsets of 96 trials each so that each combination of variables occurred once in each subset. Stimuli were presented centrally on a light-grey background. Viewing distance was not controlled but approximated 60 cm. Participants pressed a left-key (the “Q”-key of an QWERTZ keyboard) for small, solid, and x-shaped stimuli and a right-key (the “P”-key) for large, dashed, and +-shaped stimuli. The spacebar served as start key.

2.3 Procedure

After giving informed consent, participants were provided with on-screen instructions in which the tasks, cues and corresponding responses were explained¹. To encourage participants to engage in MI, an electrode was connected to their right index finger, which was attached to a bogus

¹ It should be noted that individual eye blink rates were measured before and after the experiment for explorative reasons. However, as the respective analyses yield no additional clear-cut information and the results pattern is not influenced by differences in eye blink rates, these results will not be reported further.

device (see Scheil & Liefoghe, 2018; Theeuwes et al., 2018, for a similar procedure). Participants were told that we were able to measure the degree to which they performed MI. In addition, a fake calibration phase was conducted in which the bogus device was tested. All responses were made with the right index finger. The experiment was run in a single session that took about 75 minutes. A practice phase of 72 trials was followed by 6 blocks of 64 trials each. Blocks were shorter than the 96 trial subsets to prevent fatigue effects.

Each trial was initiated by participants pressing the spacebar. If the spacebar was not already pressed at the beginning of the trial, the request “Leertaste” (spacebar in German) was presented in the center of the screen until pressing of the spacebar or until a maximum time of 3,000ms had elapsed. If the spacebar was already pressed at the beginning of the trial, this display was not presented. When the spacebar was pressed, a fixation cross was displayed for 1,000ms, followed by the cue and imperative stimulus that remained visible until participants pressed the spacebar again to end the trial or until 3,000ms had elapsed. On overt trials, participants were required to release the spacebar, press the response key and return to the spacebar. On covert trials, the spacebar had to be released. After that, participants had to imagine the movement without actually moving the finger towards the response keys. The spacebar had to be pressed when the imagined movement was finished. Pressing the spacebar again terminated the trial and initiated the next one. At the end of each block, participants received error feedback. To simulate registration of imagined movements with the bogus device, the amount of errors made on the overt trials was doubled for the feedback (e.g., if a participant made two errors in the overt condition, the error amount in the feedback was four).

2.4 Design and data analysis

The practice phase was excluded from analyses, as were the first two trials of each block. In addition, invalid trials (in which the spacebar was not released or not pressed again, or in which a key was pressed that did not belong to the set of response keys, 3.4 % in total) were discarded. In the main analyses we focus on the time interval between the stimulus onset and the participants

pressing the rest-key after responding overtly or covertly. We refer to this interval as Reaction Times. Nevertheless, Reaction Times can be decomposed into Release Times (i.e., the time between the stimulus onset and releasing the rest-key) and Inter Rest-Key Intervals (i.e., the time between releasing and re-entering the rest-key). Separate analyses of Release Times and Inter Rest-Key Intervals are given in the appendix. A schematic illustration of the different time frames is presented in Figure 1. Because error data was not available in the covert trials, errors (as defined as pressing the incorrect key) were not discarded from the overt trials.

Figure 1 about here

First, correlations between overt and covert responses were determined to check whether participants really engaged in MI. This was done for all conditions of the following ANOVA separately. After that, the response mode (covert or overt) in trials n and $n - 1$ and its influence on $n - 2$ repetition costs was analyzed. Reaction Times were subjected to a repeated measures ANOVA with the subjects factors Task Sequence (ABA vs. CBA), Mode (overt vs. covert), and lag1-Mode (overt vs. covert).

However, when taking $n - 2$ repetition costs into account, not only features of the current trial but aspects of all three trials involved in the task sequence may affect the results. In a sequence of three trials that serves to investigate $n - 2$ repetition costs, the task in trial $n - 2$ is the one that is assumed to be inhibited to reduce interference. The more activated the task, the more it interferes with the task in the following trial and the more it has to be inhibited (see Scheil & Kleinsorge, 2014). Therefore, the response mode in trial $n - 2$ is of interest for observing effects of MI on the activation of tasks. In addition, after the response has been executed in trial $n - 2$, inhibition can start during preparation for the task in trial $n - 1$. As such, the response mode in trial $n - 1$ is also of interest for observing effects of MI on the inhibition of tasks.² In view of these considerations, a second analysis was added in which the response mode (covert or overt) in trials $n - 2$ and $n - 1$ was taken into

² An analysis including the response mode in trial n , $n - 1$, and $n - 2$ was avoided due to less than 30 observations per cell that were left. However, as this analysis did not yield a four-way interaction of all factors, no information is lost by reporting two ANOVAs with three factors each.

account. More precisely, Reaction Times were analyzed using an ANOVA with the within-subjects factors Task Sequence (ABA vs. CBA), lag1-Mode (overt vs. covert), and lag2-Mode (overt vs. covert).

Finally, in line with previous studies investigating MI in the context of cognitive-control tasks (e.g., Rieger et al., 2017; Scheil & Liefoghe, 2018) we also investigated response-repetition effects following covert and overt trials. If specific motor-command inhibition underlies MI, response repetitions should be more affected by MI than response switches. For this purpose, an ANOVA with the within-subjects factors Mode (overt vs. covert), lag1-Mode (overt vs. covert), and Response Transition (repetition vs. switch) were conducted. For these analyses, invalid trials not only in the current but also in the previous trial were excluded to prevent the Response Transition factor from being contaminated.

3. Results

3.1. Manipulation Check Analysis

In order to check whether participants did perform MI on covert trials, for each participant the correlation between Reaction Times on covert trials and Reaction Times on overt trials was calculated across all remaining experimental conditions that resulted from a factorial combination of Task Sequence, lag1-Mode, and lag2-Mode (see Guillot et al., 2012b for a discussion of this approach). These correlations were significant, ranging from $r = .92$ to $r = .98$, all p 's $< .001$. This corroborates that participants did engage in MI on covert trials as intended.

3.2. Mode in trial n and $n - 1$

Means and standard errors are depicted in Figure 2. The analysis yielded a significant main effect of Task Sequence, $F(1, 29) = 4.26$, $p < .05$, $\eta_p^2 = .13$, $MSe = 6,622$, reflecting mean $n - 2$ repetition costs of 22ms. Furthermore, the main effect of Mode was significant, $F(1, 29) = 19.89$, $p < .001$, $\eta_p^2 = .41$, $MSe = 600,011$, because participants responded faster in overt (2414ms) than in covert (2860ms) trials. Both factors interacted, $F(1, 29) = 4.41$, $p < .05$, $\eta_p^2 = .13$, $MSe = 6,831$. Significant ($p < .001$,

Newman-Keuls-corrected) $n - 2$ repetition costs of 44ms were observed for overt responses in the current trial, whereas in covert trials, no such costs (1ms, $p > .95$) were visible. In addition, the interaction of Task Sequence and lag1-Mode was significant, $F(1, 29) = 21.11$, $p < .001$, $\eta_p^2 = .42$, $MSe = 6,298$. After covert responses in trial $n - 1$, significant ($p < .001$) $n - 2$ repetition costs of 69ms were visible, whereas after overt responses, a marginally significant ($p < .10$) $n - 2$ repetition benefit of 26ms occurred. In addition, Mode and lag1-Mode interacted, $F(1, 29) = 7.55$, $p < .05$, $\eta_p^2 = .21$, $MSe = 27,333$. The mode effect (covert minus overt) was larger after overt (505ms) than after covert trials (387ms). The three-way interaction of all factors was not significant, $p > .10$.³

3.3. Mode in trial $n - 1$ and $n - 2$

Means and standard errors are depicted in Figure 3. This analysis yielded a significant main effect of Task Sequence, $F(1, 29) = 10.65$, $p < .01$, $\eta_p^2 = .27$, $MSe = 6,206$, reflecting mean $n - 2$ repetition costs of 33ms. Moreover, the main effect of lag2-Mode was significant, $F(1, 29) = 16.00$, $p < .001$, $\eta_p^2 = .36$, $MSe = 10,425$. Responses were slower after overt (2675ms) than after covert responses in trial $n - 2$ (2613ms). The two-way interaction of Task Sequence and lag1-Mode was significant as well, $F(1, 29) = 7.00$, $p < .05$, $\eta_p^2 = .19$, $MSe = 8,131$. After covert trials, large $n - 2$ repetition costs of 64ms occurred, whereas this was not the case after overt trials (2ms). The three-way interaction of all factors was not significant, $p > .16$.

3.4. Response repetition effects after covert and overt trials⁴

Only effects involving the Response Transition factor are reported. The main effect of Response Transition was significant, $F(1, 29) = 10.72$, $p < .01$, $\eta_p^2 = .27$, $MSe = 5,357$, due to a mean response repetition cost of 31ms. Furthermore, Response Transition interacted with lag1-Mode, $F(1,$

³ Please note that the data pattern remains unchanged if errors and post-error trials are removed for overt responses. The F values even increase, leading to a significant three-way interaction, $F(1, 29) = 4.63$, $p < .05$, $\eta_p^2 = .14$, $MSe = 71,166$: $n - 2$ repetition costs were present after covert trials, irrespective of the response mode in the current trial. After overt trials, $n - 2$ repetition costs were only visible for overt trials, while an $n - 2$ repetition benefit occurred for covert trials.

⁴ A combined analysis with the factors Task Sequence, Mode, lag1-Mode, and Response Transition revealed that the Response Transition factor did affect neither the interaction of Task Sequence and Mode nor the interaction of Task Sequence and lag1-Mode ($p > .82$ and $p > .21$ for the respective three-way interactions).

29) = 10.58, $p < .01$, $\eta_p^2 = .27$, $MSe = 5,545$. Whereas after overt trials in $n - 1$, a large response repetition cost of 62ms occurred, no response repetition effects (0ms) were visible after covert trials. In addition, the three-way interaction of all factors was significant, $F(1, 29) = 6.85$, $p < .05$, $\eta_p^2 = .19$, $MSe = 5,400$ (cf. Figure 4). For overt trials, response repetition effects were of about the same size after overt (51ms) and covert (38ms) trials. For covert trials, on the contrary, response repetition costs of 74ms were visible after overt trials that turned into a benefit of 39ms after covert trials.

Figure 4 about here

4. Discussion

Whereas previous studies suggested that MI leads to the inhibition of motor commands (e.g., Rieger et al., 2017; Scheil & Liefoghe, 2018), the central aim of the present study was to investigate whether MI can also lead to the inhibition of the complete task-set, which underlies a particular action or task. To this end, a task-switching experiment with three tasks was designed in which participants responded overtly via keypresses to half of the trials and covertly via MI to the other half. As such, we could use $n - 2$ repetition costs as a proxy of task-set inhibition. Before considering the results in detail, it is important to first indicate that the correlation between overt and covert responses was highly significant, suggesting that participants engaged in MI, as was intended by our procedure. In addition, the overall pattern of results suggested the presence of $n - 2$ repetition costs when trial $n - 1$ required a covert response. In view of the findings of Schuch and Koch (2003), who did not observe $n - 2$ repetition costs when trial $n - 1$ was a No-Go trial, this pattern of results again suggests that participants actually engaged in MI instead of just waiting until a covert trial was over.

Having established that participants engaged in MI as we intended, we treat our results in more detail. First, $n - 2$ repetition costs were significant when the current trial was an overt one, replicating the standard effect of the presence of $n - 2$ repetition costs. However, if the current trial was a covert one, no $n - 2$ repetition costs were visible. More importantly, the $n - 2$ repetition cost was significantly modulated by the response mode on trial $n - 1$: $n - 2$ repetition costs were larger when trial $n - 1$ was a covert trial, compared to when this trial was an overt trial. This finding

supports the hypothesis that MI amplifies the degree of task-set inhibition, rather than calling upon a different type of inhibition which competes for the same resources (cf., Verbruggen et al., 2004, 2006a, 2006b). Although previous behavioral research suggested that MI is associated with a global inhibition of motor commands (e.g., Rieger et al., 2017; Scheil & Liefoghe, 2018), which is in line with the literature on MI in the domain of motor control (e.g., Guillot et al., 2012), the current findings rather suggest that the inhibitory mechanism during MI not only targets motor commands, but also affects the whole task-set underlying the task that needs to be performed covertly. Pursuing this assumption, the question arises how exactly the inhibitory mechanism associated with MI, may target task-sets. We propose that MI may entail the recruitment of a neural inhibitory network, which in turn affects other cognitive processes. This network may include the subthalamic nucleus, which is supposed to play a role in motor suppression due to its direct afferents from motor and premotor areas (Haynes & Haber, 2013; Nambu, Tokuno, Inase, & Takad, 2007). Furthermore, prior research suggests that the subthalamic nucleus is involved in a frontal-basal ganglia circuit that also affects cognitive performance, like working memory (Wessel et al, 2015). Therefore, a possible explanation for the present results is that during MI, motor and premotor areas activate the subthalamic nucleus, which in turn leads to inhibition of the motor signal and, additionally, fires to prefrontal regions, leading to inhibition of (at least parts of) the task-set. Of course, this assumption is speculative at the moment and has to be examined in the future.

The present results also need to be considered in view of the distinction between response selection and response preparation (e.g., Philipp, Jolicoeur, Falkenstein, & Koch, 2007). Philipp and colleagues investigated this distinction by measuring $n - 2$ repetition costs in a go/no-go procedure. These authors observed reduced $n - 2$ repetition costs when trial $n - 1$ contained a no-go trial with a long go-signal delay, that is, after trials in which a response was prepared (due to the long signal delay) but not executed. This result was interpreted in terms of response execution (instead of response selection only) in trial $n - 1$ being a necessary prerequisite for $n - 2$ repetition costs to reach full extent. The present finding of sizeable $n - 2$ repetition costs after a covert trial is at odds with these results concerning no-go trials. Our findings thus suggest a distinction between stopping a

prepared response and the covert execution of a movement, thereby emphasizing the importance of investigating MI and its potential effects on cognitive-control processes.

The current results are hard to reconcile with the assumption that $n - 2$ repetition costs are a mere by-product of other processes like response selection, or that they are based on processes spreading inhibition uniformly across tasks irrespective of specific task demands. In contrast, the present results add to the body of literature characterizing the inhibition process underlying $n - 2$ repetition costs as a flexible one that exerts inhibition depending on the task environment. This was, for example, shown by Jost, Hennecke, and Koch (2017) who found $n - 2$ repetition costs to be dependent on task dominance. These authors concluded that the adjustment of employing inhibition is context-sensitive. In the same vein, Grange and Houghton (2010) showed that $n - 2$ repetition costs are affected by different kinds of cue-target translations leading to different amounts of task conflict. These results point out that $n - 2$ repetition costs rely on a flexible and adaptive inhibition process. More research is needed to understand the characteristics of this process in more detail.

An additional comment needs to be made on the results of the response-repetition effects. An overall response-repetition cost was visible after overt trials that was absent after covert trials. The cost after overt trials is in line with previous research on response repetition effects showing a repetition benefit for task repetitions only, whereas for task switches (which were present throughout the experiment) a repetition cost occurs (e.g., Kleinsorge, 1999). In contrast, no overall cost was observed after covert trials, resulting in a two-way interaction. For covert responses following covert ones, the three-way interaction even showed a reversal of the typical response repetition effect, with response repetitions going along with a benefit instead of a cost. Relating these results to the different inhibitory processes possibly underlying MI proposed by Guillot and colleagues (2012), they provide, consistent with the results of Rieger et al. (2017) as well as Scheil and Liefoghe (2018), evidence for specific motor-command inhibition but not for global motor-command inhibition. Considering these results from another point of view, they can also be related to the feature integration account of Hommel (2005). According to this account, stimulus and response features are integrated into a common event file. The chance of integrating a certain

feature depends on its activation level. It is also assumed that binding may depend on a success signal as generated by a correct response. The response repetition benefit that was visible after two successive covert trials can be explained by assuming a lower activation level of a covert in contrast to an overt response and/or the absence of a success signal without an overt response that prevented response features from being integrated into an episode. As a consequence, the typical response repetition cost for task switches, which can be explained by a partial mismatch of the old and the new episode in case of a successful feature integration process, failed to accrue.

Another prominent account to explain response repetition effects in task switching is the response inhibition account put forward by Hübner and colleagues (e.g., Hübner & Druey, 2006; 2008; Steinhauser, Hübner, & Druey, 2009). It assumes that every response is inhibited after execution to prevent accidental re-execution, leading to response repetition costs. When the task repeats, however, these costs are outweighed by positive priming of the stimulus category. This inhibitory process was further analyzed by Steinhauser and colleagues (2009) using the lateralized readiness potential (LRP), an event-related potential considered as correlate of motor preparedness. They found an LRP bias towards the alternative response during preparation time, which was taken as evidence for the inhibition of abstract response codes (like “left” or right”) to control motor preparedness. A possible explanation of the present result of reversed response repetition effects after C-C sequences is that MI does not result in an LRP bias, yielding no cost when the same response has to be imagined again. However, such an absence of the LRP bias could be due to either subthreshold motor command or to motor-command inhibition caused by MI.

Taken together, we obtained evidence for the hypothesis that MI entails the inhibition of abstract task-set representations. When considering the present results in view of the two possible mechanisms underlying MI proposed by Jeannerod (2001; see also Guillot et al., 2012), our results again favor the hypothesis that overt movements during MI are avoided by means of inhibitory processes, possibly being involved in a broad neural inhibitory network. In contrast, no evidence could be found for subthreshold motor commands underlying MI. This is in line with the results of

Rieger and colleagues (2017) as well as of Scheil and Liefoghe (2018) who also concluded that inhibition instead of subthreshold motor commands guides MI. The added value of the current study, compared to the work of Rieger et al. (2017) and Scheil and Liefoghe (2018), is that we have more clear evidence indicating that inhibition in MI not only takes place at the level of motor commands, but also on the more abstract level of the task-set underlying a particular task.

Conflict of interest:

The authors declare that they have no conflict of interest.

Ethical Standards:

The present study was performed in accordance with the ethical standards laid down the Declaration of Helsinki and approved by the Ethical Committee of IfADo.

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Figure Captions

Figure 1: Overview of the procedure of single trials.

Figure 2: Mean Reaction Times [ms] as a function of Task Sequence (ABA vs. CBA), Mode (Overt vs. Covert), and lag1-Mode (Overt vs. Covert). Vertical bars represent SEM.

Figure 3: Mean Reaction Times [ms] as a function of Task Sequence (ABA vs. CBA), lag1-Mode (Overt vs. Covert), and lag2-Mode (Overt vs. Covert). Vertical bars represent SEM.

Figure 4: Mean Inter Rest-Key Intervals [ms] as a function of Response Transition (Response Repetition vs. Response Switch), Mode (Overt vs. Covert), and lag1-Mode (Overt vs. Covert). Vertical bars represent SEM.

Figure 1

Figure 2

Figure 3

Figure 4

Appendix

Separate analyses of Release Times and Inter Rest-Key Intervals

As in the main results, correlations between overt and covert responses were determined in a first step. This was done for all conditions of the following ANOVA separately. After that, both dependent measures were subjected to a repeated measures ANOVA with the subjects factors Task Sequence (ABA vs. CBA), Mode (overt vs. covert), and lag1-Mode (overt vs. covert). In a second step, RTs and IRKIs were analyzed using an ANOVA with the within-subjects factors Task Sequence (ABA vs. CBA), lag1-Mode (overt vs. covert), and lag2-Mode (overt vs. covert).

Release Times (RTs)

Manipulation Check Analysis

In order to check whether participants did perform MI on covert trials, for each participant the correlation between RT on covert trials and RT on overt trials was calculated. These correlations were significant, ranging from $r = .88$ to $r = .94$, all p 's $< .001$. This corroborates that participants did engage in MI on covert trials as intended.

Main Analysis

Regarding the main analysis, the main effect of lag1-Mode was significant, $F(1, 29) = 6.47$, $p < .05$, $\eta_p^2 = .16$, $MSe = 15,841$. Mean RTs were higher after overt (971 ms) than after covert trials (930 ms). Furthermore, the three-way interaction of Task Sequence, lag1-Mode, and lag2-Mode was significant, $F(1, 29) = 5.92$, $p < .05$, $\eta_p^2 = .17$, $MSe = 2,666$. For overt responses in trial $n - 2$, no $n - 2$ repetition costs were visible irrespective of whether the response in trial $n - 1$ had to be executed overtly or covertly (11 and 1 ms, p 's $> .68$). For covert responses in trial $n - 2$, however, large and significant ($p < .05$) $n - 2$ repetition costs were visible for covert responses in trial $n - 1$ (39 ms) whereas no such costs emerged for overt responses in trial $n - 1$ (-15 ms, $p > .48$).

Inter Rest-Key Intervals (IRKIs)

Manipulation Check Analysis

As for RTs, individual correlations between IRKIs on covert trials and IRKIs on overt trials across all conditions were calculated in a first step. These correlations ranged from $r = .62$ to $r = .70$, all p 's $< .001$.

Main Analysis

Coming to the main analysis, overall marginally significant $n - 2$ repetition costs of 24 ms were visible, $F(1, 29) = 3.67$, $p < .07$, $\eta_p^2 = .11$, $MSe = 9,583$. The main effect of lag1-Mode was significant, $F(1, 29) = 9.18$, $p < .01$, $\eta_p^2 = .24$, $MSe = 25,090$, due to higher IRKIs after covert (1725 ms) than after overt responses (1663 ms). Furthermore, the main effect of lag2-Mode was significant, $F(1, 29) = 17.02$, $p < .001$, $\eta_p^2 = .37$, $MSe = 11,042$, due to higher IRKIs after overt responses in trial $n - 2$ (1722 ms) compared with covert responses in trial $n - 2$ (1666 ms). The interaction of Task Sequence and lag1-Mode was marginally significant, $F(1, 29) = 3.72$, $p < .07$, $\eta_p^2 = .11$, $MSe = 6,216$, due to a tendency towards higher $n - 2$ repetition costs after covert (44 ms) than after overt (5 ms) trials. Most importantly, the three-way interaction of all factors was significant, $F(1, 29) = 6.62$, $p < .05$, $\eta_p^2 = .19$, $MSe = 9,513$. Large $n - 2$ repetition costs were visible for covert trials in $n - 1$ that were preceded by an overt trial (92 ms), while in the other conditions, no significant $n - 2$ repetition costs could be observed (-12 ms for overt-overt trials, 21 ms for covert-overt trials, and -5 ms for covert-covert trials, all p 's $< .40$, Newman-Keuls corrected).

Discussion

Regarding Release Times, $n - 2$ repetition costs were most pronounced when a covert response in trial $n - 2$ was followed by another covert response in trial $n - 1$. This effect yields first support for the notion that processes underlying MI and $n - 2$ repetition costs interact with each other.

For IRKIs, $n - 2$ repetition costs were of large size when an overt response in trial $n - 2$ was followed by a covert response in trial $n - 1$. This is in line with the supposition that a high necessity to inhibit the task due to a high amount of activation of that task in trial $n - 2$ as well as the opportunity to employ inhibition during trial $n - 1$ are needed to cause high $n - 2$ repetition costs (cf. Scheil & Kleinsorge, 2014). Overt responding in trial $n - 2$ led to a full activation of the whole task set, including all response parameters. Covert responding in trial $n - 1$ caused an interaction of inhibition processes due to MI-induced inhibition of overt responding and task inhibition due to high interference of the task in trial $n - 2$. This concurrence of both inhibition processes in turn caused high $n - 2$ repetition costs.