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RESEARCH

Towards formal models of inhibitory mechanisms involved in motor imagery: a commentary on Bach et al. (2022)

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Abstract

A vast body of research suggests that the primary motor cortex is involved in motor imagery. This raises the issue of inhibition: how is it possible for motor imagery not to lead to motor execution? Bach et al. (Psychol Res Psychol Forschung. 10.1007/s00426-022-01773-w, 2022, this issue) suggest that the motor execution threshold may be "upregulated" during motor imagery to prevent execution. Alternatively, it has been proposed that, in parallel to excitatory mechanisms, inhibitory mechanisms may be actively suppressing motor output during motor imagery. These theories are verbal in nature, with well-known limitations. Here, we describe a toy-model of the inhibitory mechanisms thought to be at play during motor imagery to start disentangling predictions from competing hypotheses.

A large body of behavioural, electrophysiological, and neuroimaging empirical evidence suggests that the motor system is involved during motor imagery (for review, see Guillot et al., 2012). This raises the "problem of inhibition of execution" (Jeannerod, 2001): Given the involvement of the motor system in motor imagery, how is it possible for motor imagery not to lead to motor execution? It has been proposed that this may be achieved by modulating (e.g. upregulating) the execution threshold (e.g. Bach et al., 2022, this issue). Alternatively, parallel inhibitory processes may prevent execution during motor imagery (Berthoz, 1996; Guillot et al., 2012). These proposals are formulated as verbal theories, with well-known limitations (Smaldino, 2020; van Rooij & Blokpoel, 2020). Notably, these theories are insufficiently specified at the algorithmic level, and can be implemented in several formal models whose predictions may concur or conflict. Here, we describe a novel algorithmic toy-model of inhibitory mechanisms presumably at play during motor imagery and use it to clarify the predictions from competing hypotheses.

The toy model provides a simplified overarching description of how the motor system is involved over time during motor imagery, roughly corresponding to the activity of populations of excitatory and inhibitory neurons. In its current formulation, this toy model is not equipped to distinguish between different forms of inhibition occurring at the cortical, subcortical, or spinal levels (Guillot et al., 2012). The overall model structure is loosely inspired from the activation threshold model of response inhibition (MacDonald et al., 2014, 2017). One important difference with the activation threshold model, however, is that here the overall level of *activation* is modelled throughout an entire trial[1] to account for both reaction times (i.e. the time it takes to prepare and initiate motor imagery) and movement times (i.e. the time it takes to imagine an action) (Fig. 1). In line with the "threshold upregulation hypothesis" of Bach et al., (2022, this issue), we expect *inhibition* to modulate the motor execution threshold during motor imagery.

The overall level of activation is modelled as a rescaled lognormal function defined as:

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[1] Here "trial" refers to a prototypical trial in the action-mode switching paradigm (Rieger et al., 2017), where participants have to perform motor imagery and indicate the onset (reaction time) and duration (movement time) of motor imagery via a response button.

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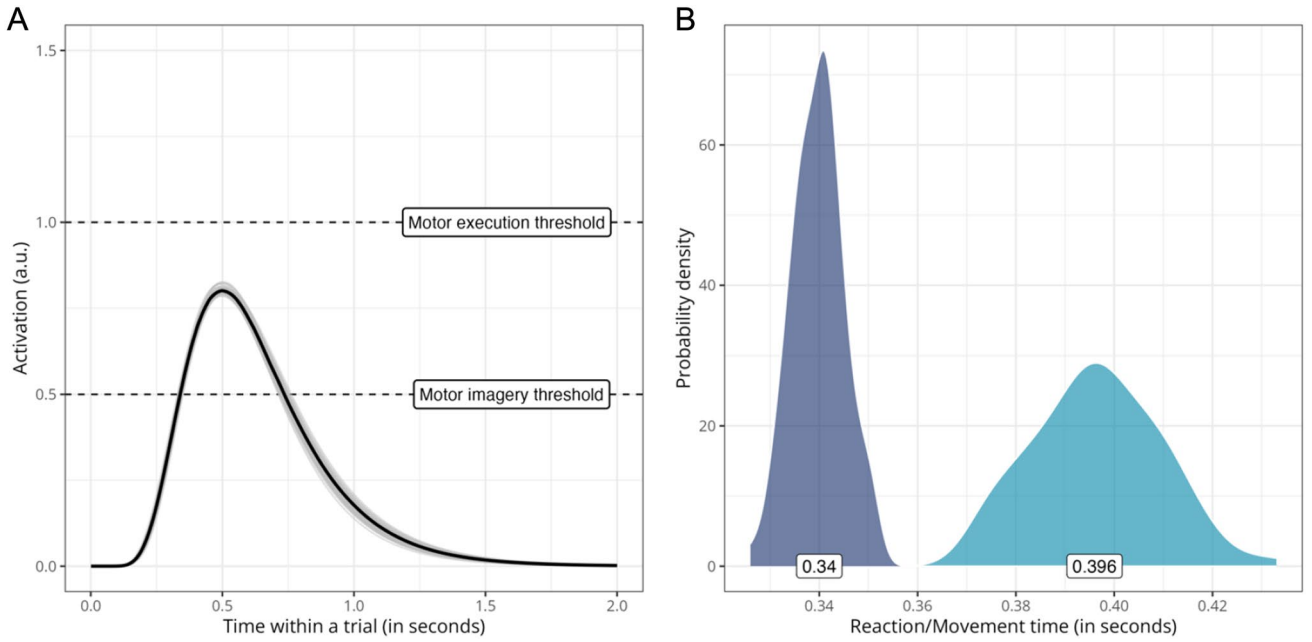

Fig. 1 Schematic overview of the model and its predictions. **A** The black line represents the average value of the activation function over the time course of a trial, grey lines represent the value of the activation function in each single trial. Reaction time is defined as the time at which the activation function crosses the threshold for motor imagery. Imagined movement times are defined as the time "spent" above this threshold (i.e. the difference between the offset and the onset). **B** Distributions of reaction times (left) and movement times (right) in motor imagery as generated by the model's architecture. Between-trial variability in reaction and movement times is caused by adding a slight amount of Gaussian noise in the model's parameters

$$f(t;A,\mu,\sigma) = A \cdot \exp\left[-\frac{(\ln t - \mu)^2}{2\sigma^2}\right], \quad t > 0 \tag{1}$$

where A and μ respectively denote the peak amplitude and peak latency of the function; σ corresponds to its width. From a neurophysiological perspective, A is thought to result from the temporal and spatial summation of excitatory inputs onto the alpha motoneuron pool, and σ is thought to reflect the speed of neuronal firing (MacDonald et al., 2017) (Fig. 1, left panel). From a psychological perspective, during motor imagery, A may be related to the vividness of motor imagery percepts, μ may be related to the speed at which these mental percepts are established, and σ may be related to their duration. The model also assumes two threshold parameters, for motor imagery (parameter m) and for motor execution (parameter r), to account for the onset and duration of imagined movements. The value of the motor imagery threshold is expressed as a fraction of the motor execution threshold. We adapt the idea of a dual threshold from recent models integrating action and decision-making (Dendauw et al., 2023; Servant et al., 2021).

Analytic solutions for both predicted response time (RT) and movement time (MT) can be derived from our toy model. If the peak amplitude A of the activation function is larger than the motor imagery threshold m, which is a necessary condition of our model to produce imagery, RT and MT for imagined trials are given by:

$$RT = \exp\left(\mu - \sigma\sqrt{2\ln(A/m)}\right) \tag{2}$$

$$MT = 2\exp(\mu) \cdot \sinh\left(\sigma\sqrt{2\ln(A/m)}\right) \tag{3}$$

This preliminary formulation allows assessing the influence of modulating the motor execution threshold, and therefore confronting more explicitly the mechanism proposed by Bach et al., (2022, this issue) with the data. Consider Fig. 2 and the interactive application linked in the "Availability of data and materials" statement. Upregulating (downregulating) the motor execution threshold will necessarily increase (decrease) the RT and decrease (increase) the MT. Therefore, longer RTs and MTs following imagined responses observed in the action-mode switching experiments (e.g. Bart et al., 2020, 2021a, 2021b; Rieger et al., 2017) cannot be explained by an inter-trial modulation of the motor execution threshold. Similarly, modulating the amplitude (i.e. the height of the activation function) alone cannot account for such effects. However, joint modulations of the amplitude and the curvature, or more parsimoniously, modulations of the peak time, can account for these effects. Indeed, all other things being equal, increasing the peak

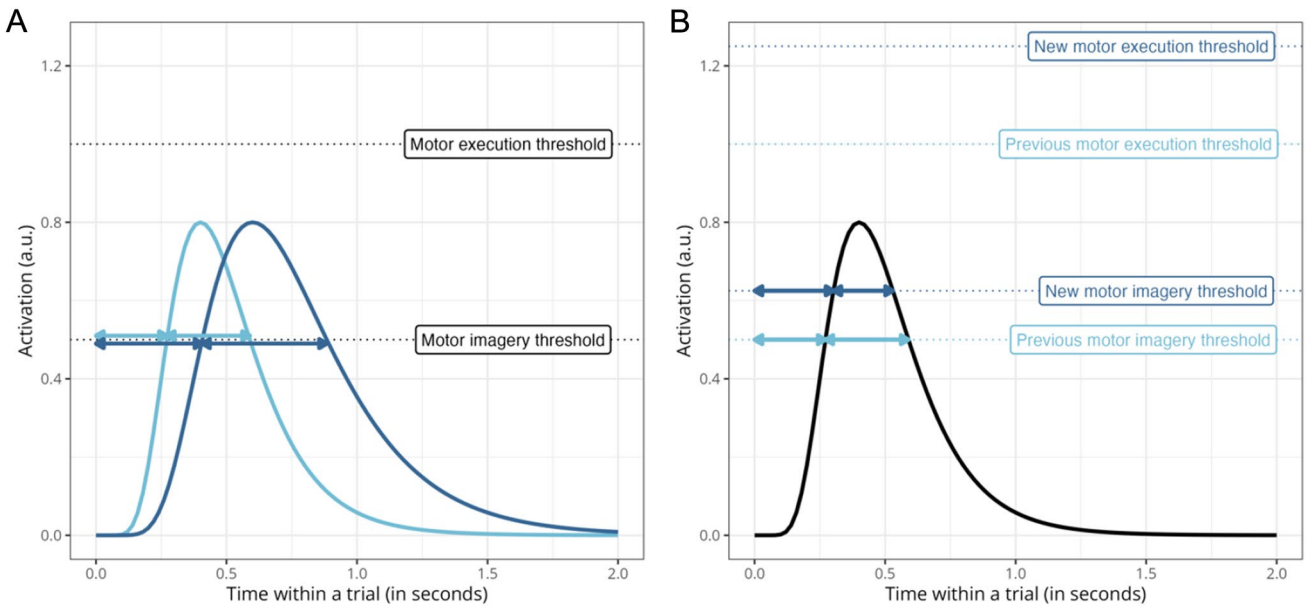

Fig. 2 Impact of varying the peak time (**A**) or the motor thresholds (**B**) on the reaction time and movement time. **A** The impact of having a later peak time (represented by the dark blue density) as compared to a shorter peak time (represented by the light blue density) will increase both the reaction time (represented by the length of the leftmost horizontal arrow), and the movement time (represented by the length of the rightmost horizontal arrow). **B** The impact of having a higher motor threshold (here the dark blue horizontal dotted line), as compared to a lower motor threshold (here the light blue horizontal dotted line), will increase the reaction time (represented by the length of the leftmost horizontal arrow) but decrease the movement time (represented by the length of the rightmost horizontal arrow)

time will increase both the predicted RT and MT (Fig. 2). Therefore, this model suggests that the aftereffects observed in action-mode switching experiments cannot be accounted by a modulation of the motor execution threshold alone but that they are compatible with a "shift" in the peak time.[2] In other words, inhibition in the previous trial may slow down the accumulation of excitatory input in the next trial, rather than "modulating the execution threshold", as suggested by Bach et al., (2022, this issue). It should be noted that a full parameter recovery study and a more extensive application of this model to empirical data is ongoing.

Beyond providing an explanation of extant data, this model can be used to generate novel predictions, for instance about motor imagery strength or vividness. In the same way that the evidence accumulated during a decision-making task has been suggested to reflect sensory vividness (Pereira et al., 2022), the maximum value (or the integral of the surface above the threshold) of the activation function can be linked to the vividness of subjective percepts associated with motor imagery. In addition, the value of this function throughout the trial can be related to modulations of EMG activity or cortical excitability recorded during motor imagery. Such predictions could be assessed in future studies combining the action-mode switching paradigm with EMG measurements and introspective scales assessing the vividness of motor imagery percepts.

In summary, our goal with this proposal is to help disambiguating the description of the mechanisms that prevent execution during motor imagery. Much remains to be discovered; as a step in these directions, we provided a simple framework for clarifying some of these verbal descriptions, with the hope of stimulating future discussion and a detailed characterization of the cognitive and neural mechanisms involved in preventing motor execution during motor imagery.

[2] This argument holds for any activation function that increases until a certain point in time and then decreases, and therefore is not specific to the lognormal activation function.

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Availability of data and materials An interactive Shiny application allowing to visualise the predictions of the model is available at: https://barelysignificant.shinyapps.io/motor_imagery_inhibition_model/. An R package providing helper functions to fit the model and visualise its predictions is available at: https://github.com/lnalborczyk/momimi.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval Not applicable.

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