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Towards formal models of inhibitory mechanisms involved in motor imagery

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17

Abstract

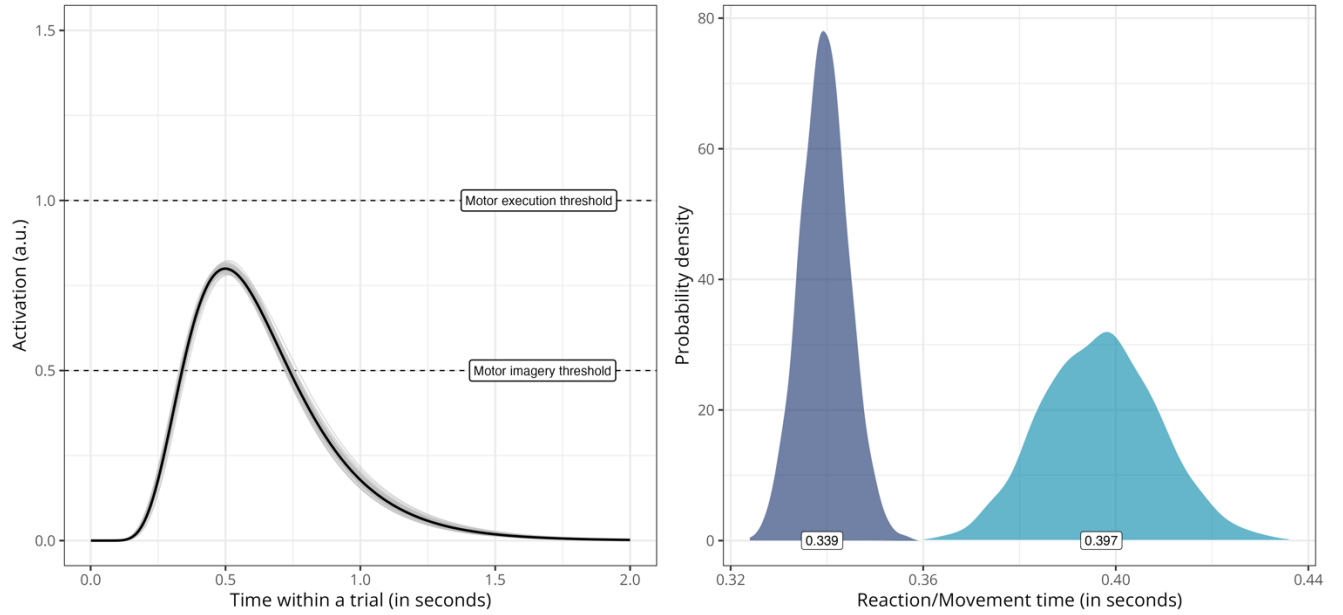
18 A vast body of research suggests that the primary motor cortex is involved during motor
19 imagery. This raises the issue of inhibition: Given the role of the motor system in providing the
20 multisensory content of motor imagery, how is it possible for motor imagery not to lead to
21 motor execution? Bach et al. (2022, this issue) suggest that the motor execution threshold may
22 be “upregulated” during motor imagery to prevent execution. Alternatively, it has been
23 proposed that, in parallel to excitatory mechanisms, inhibitory mechanisms may be actively
24 suppressing motor output during motor imagery. These theories are verbal in nature, with
25 well-known limitations. Here, we describe a toy-model of the inhibitory mechanisms thought
26 to be at play during motor imagery to start disentangling predictions from competing
27 hypotheses.

28 *Keywords:* motor imagery, motor inhibition, response inhibition, computational
29 modelling, cognitive modelling

30

31 A large body of behavioural, electrophysiological, and neuroimaging empirical evidence
32 suggests that the motor system is involved during motor imagery (for review, see Guillot et al.,
33 2012). This raises the "problem of inhibition of execution" (Jeannerod, 2001): Given the role of
34 the motor system in providing the multisensory content of motor imagery, how is it possible
35 for motor imagery not to lead to motor execution? It has been proposed that this may be
36 achieved by modulating (e.g., upregulating) the execution threshold (e.g., Bach et al., 2022, this
37 issue). Alternatively, parallel inhibitory processes may prevent execution during motor
38 imagery (Berthoz, 1996; Guillot et al., 2012). These proposals are formulated as verbal theories,
39 with well-known limitations (Smaldino, 2020; van Rooij & Blokpoel, 2020). Notably, these
40 theories are insufficiently specified at the algorithmic level, and can be implemented in several
41 formal models whose predictions may concur or conflict. Here, we describe an algorithmic
42 toy-model of inhibitory mechanisms presumably at play during motor imagery and use it to
43 clarify the predictions from competing hypotheses.

44 The toy model provides a simplified overarching description of how the motor system is
45 involved over time during motor imagery, roughly corresponding to the activity of populations
46 of excitatory and inhibitory neurons (MacDonald et al., 2014, 2017). In its current formulation,
47 this toy model is not equipped to distinguish between different forms of inhibition occurring
48 at the cortical, subcortical, or spinal levels (Guillot et al., 2012). The overall model structure is
49 adapted from the activation threshold model of response inhibition (MacDonald et al., 2014,
50 2017). One important difference with the activation threshold model, however, is that here the
51 overall level of *activation* is modelled throughout the entire trial to account for both reaction
52 times (i.e., the time it takes to prepare and initiate execution/imagery) and movement times
53 (i.e., the time it takes to execute/imagine an action) (Figure 1). In line with the "threshold
54 upregulation hypothesis" of Bach et al. (2022, this issue), we expect *inhibition* to modulate the
55 motor execution threshold during motor imagery.



56

57 *Figure 1. Schematic overview of the model and its predictions. Left: the black line represents the*
 58 *average value of the activation function over the time course of a trial, grey lines represent the*
 59 *value of the activation function in each single trial. Reaction time is defined as the time at which*
 60 *the activation function crosses the threshold for motor execution (in executed trials) or for motor*
 61 *imagery (in imagined trials). Imagined and executed movement times are defined as the time*
 62 *“spent” above this threshold (i.e., the difference between the offset and the onset). Right:*
 63 *Distributions of reaction times and imagined movement times generated by the model's*
 64 *architecture. Between-trial variability in reaction and movement times is caused by adding a*
 65 *slight amount of Gaussian noise in the model's parameters.*

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

$$67 \quad f(t; A, \mu, \sigma) = A \cdot \exp \left[-\frac{(\ln t - \mu)^2}{2\sigma^2} \right], \quad t > 0 \quad (1)$$

68 where A and μ respectively denote the peak amplitude and peak latency of the function;
 69 σ corresponds to its width. From a neurophysiological perspective, A is thought to result from

70 the temporal and spatial summation of excitatory inputs onto the alpha motoneuron pool, and
 71 σ is thought to reflect the speed of neuronal firing (lower values of σ imply more time to attain
 72 the peak, *ceteris paribus*) (Figure 1, left panel). From a psychological perspective, during
 73 motor imagery, A may be related to the vividness of motor imagery percepts, μ may be related
 74 to the speed at which these mental percepts are established, and σ may be related to their
 75 duration. The model also assumes two threshold parameters, for motor imagery (parameter
 76 m) and for motor execution (parameter r) respectively, to account for the onset and duration
 77 of imagined or executed movements. The value of the motor imagery threshold is expressed as
 78 a fraction of the motor execution threshold. We adapt the idea of a dual threshold from recent
 79 models integrating action and decision-making (Dendauw et al., 2022; Servant et al., 2021).

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

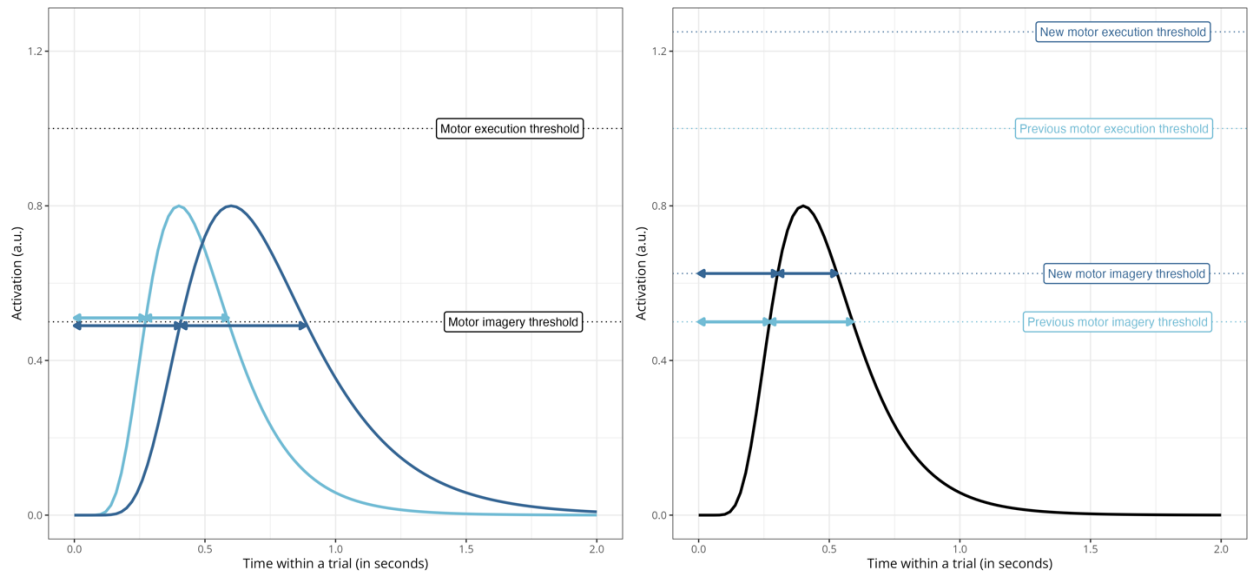
$$84 \quad RT = \exp\left(\mu - \sigma\sqrt{2 \ln(A/m)}\right) \quad (2)$$

$$85 \quad MT = 2 \exp(\mu) \cdot \sinh\left(\sigma\sqrt{2 \ln(A/m)}\right) \quad (3)$$

86 This preliminary formulation allows assessing the influence of modulating the motor
 87 execution threshold, and therefore confronting more explicitly the mechanism proposed by
 88 Bach et al. (2022, this issue) with the data. Consider Figure 2 and the interactive application
 89 linked in the “Code availability” statement. Upregulating (downregulating) the motor
 90 execution threshold will necessarily increase (decrease) the RT and decrease (increase) the
 91 MT. Therefore, longer RTs and MTs of executed or imagined responses following imagined
 92 responses observed in the action mode switching experiments (e.g., Bart et al., 2021c, 2021a,

93 2021b; Rieger et al., 2017) cannot be explained by an inter-trial modulation of the motor
94 execution threshold. Similarly, modulating the amplitude (i.e., the height of the activation
95 function) alone cannot account for such effects. However, joint modulations of the amplitude
96 and the curvature, or more parsimoniously, modulations of the peak time, can account for
97 these effects. Indeed, all other things being equal, increasing the peak time will increase both
98 the predicted RT and MT (Figure 2). Therefore, this model tells us that the aftereffects
99 observed in action-mode switching experiments cannot be accounted by a modulation of the
100 motor execution threshold but that they are compatible with a “shift” in the peak time.¹ In
101 other words, inhibition in the previous trial may slow down the accumulation of excitatory
102 input in the next trial, rather than “modulating the execution threshold”, as suggested by Bach
103 et al. (2022, this issue). It should be noted that a full parameter recovery study and a more
104 extensive application of this model to empirical data is ongoing.

¹ 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.



105
 106 *Figure 2. Impact of varying the peak time (left) or the motor thresholds (right) on the reaction*
 107 *time and movement time. Left: the impact of having a later peak time (represented by the dark*
 108 *blue density) as compared to a smaller peak time (represented by the light blue density) will*
 109 *increase both the reaction time (represented by the length of the leftmost horizontal arrow), and*
 110 *the movement time (represented by the length of the rightmost horizontal arrow). Right: the*
 111 *impact of having a higher motor threshold (here the dark blue horizontal dotted line), as*
 112 *compared to a lower motor threshold (here the light blue horizontal dotted line), will increase the*
 113 *reaction time (represented by the length of the leftmost horizontal arrow) but decrease the*
 114 *movement time (represented by the length of the rightmost horizontal arrow).*

115 Beyond providing an explanation of extant data, this model can be used to generate
 116 novel predictions, for instance about motor imagery strength or vividness. In the same way
 117 that the evidence accumulated during a decision-making task has been suggested to reflect
 118 sensory vividness (Pereira et al., 2022), the maximum value (or the integral of the surface above
 119 the threshold) of the activation function may be predictive of the vividness of subjective
 120 percepts associated with motor imagery. In addition, the value of this function throughout the

121 trial could also be related to modulations of EMG activity or cortical excitability recorded
122 during motor imagery. This could be assessed in future studies combining the action-mode
123 switching paradigm with EMG measurements and introspective scales assessing the vividness
124 of motor imagery percepts.

125 In summary, our goal with this proposal is to help disambiguating the description of
126 the mechanisms that prevent motor activation to trigger execution during motor imagery.
127 What do we mean by stating that motor imagery is accompanied by a “subliminal activation of
128 the motor system”? Is it subliminal because multiple processes compete with one another, and
129 the result of this computation is a sub-threshold activation? Or is it because the motor
130 execution threshold is modulated? If, so, how (i.e., by which processes) is it modulated? How is
131 this implemented (e.g., at the neural or spinal level)? Much remains to be discovered; as a step
132 in these directions, we provided a simple framework for clarifying some of these verbal
133 descriptions, with the hope of stimulating future discussion and a detailed characterisation of
134 the cognitive and neural mechanisms involved in preventing motor execution during motor
135 imagery.

136

137 Code availability

138 The code underlying a preliminary version of the model and the Shiny application is
139 available at: https://github.com/lnalborczyk/motor_imagery_inhibition_model. The
140 interactive Shiny application is available at:
141 https://barelysignificant.shinyapps.io/motor_imagery_inhibition_model/.

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151 conditions.

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