

# A Revised Computational Neuroanatomy for Motor Control

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## Abstract

We discuss a new framework for understanding the structure of motor control. Our approach integrates existing models of motor control with the reality of hierarchical cortical processing and the parallel segregated loops that characterize cortical-subcortical connections. We also incorporate the recent claim that cortex functions via predictive representation and optimal information utilization. Our framework assumes each cortical area engaged in motor control generates a predictive model of a different aspect of motor behavior. In maintaining these predictive models, each area interacts with a different part of the cerebellum and basal ganglia. These subcortical areas are thus engaged in domain appropriate system identification and optimization. This refocuses the question of division of function among different cortical areas. What are the different aspects of motor behavior that are predictively modelled? We suggest that one fundamental division is between modelling of task and body while another is the model of state and action. Thus, we propose that the posterior parietal cortex, somatosensory cortex, premotor cortex, and motor cortex represent task state, body state, task action, and body action, respectively. In the second part of this review, we demonstrate how this division of labor can better account for many recent findings of movement encoding, especially in the premotor and posterior parietal cortices.

## 30 **Introduction**

31           Motor control is perhaps one of the most central and complex tasks of the brain. For example,  
32 while driving, we must move our arms, legs, and gaze in a coordinated fashion to control the movement  
33 of our car while also assessing its movement and that of the other cars around us. For that to happen our  
34 brain needs to integrate sensory and motor information about our own body's state (joint configuration)  
35 and the task state (car direction and speed) in order to plan the required action within the task (like taking  
36 a sharp turn while staying on the road and avoiding other cars) and the body action to enable it (turning  
37 the wheel with the hands and controlling the gas and brake pedals with the foot). This requires predictive  
38 coding of the outcome of movements at both the task and body level, accounting for the multiple costs of  
39 the task (maintaining the speed limit and proper distance, avoiding rapid acceleration or deceleration) and  
40 the body (keeping the arms in comfortable positions while maintaining the ability to respond). As such,  
41 the neuroanatomy of motor control involves multiple cortical and subcortical regions across the brain. For  
42 decades, theories of the motor functions have failed to address how these different regions simultaneously  
43 coordinate the body within the task. We will extend existing theories regarding the roles of the cerebral  
44 cortex, the cerebellum and the basal ganglia to address this gap. The historical focus on these three areas  
45 (e.g., Kornhuber, 1971; Mogensson et al., 1980) is justified largely because they are tightly interconnected  
46 and have been heavily studied in the context of reaching and grasping movements, finger movements, eye  
47 movements, and locomotion. Of course, other areas – most obviously the spinal cord, red nucleus, and  
48 thalamus – play key roles in motor control.

49           Kenji Doya proposed an influential hypothesis that delineated the roles of these different brain  
50 structures based on computational principles (Doya, 1999, 2000). Doya suggested that the cerebellum, the  
51 basal ganglia, and the cerebral cortex are specialized for different types of learning: supervised learning,  
52 reinforcement learning, and unsupervised learning, respectively. Doya addressed the way that these  
53 different learning rules might shape the roles each motor area played in motor behavior. His view was that  
54 the learning rules would lead the cerebellum to form internal models, the basal ganglia to play a role in  
55 action selection and the cortex to form representations of state and action. Different versions of this idea  
56 of the functions of these different areas have served the field well for many years. However, they were  
57 brought together particularly powerfully when they were connected to ideas of optimal feedback control  
58 introduced into the field by Emo Todorov and Michael Jordan. The optimal feedback control theory for  
59 motor coordination (Todorov and Jordan, 2002) suggested a mathematical approach for motor control  
60 which formalized the relationship between motor commands, task goals, sensory-motor noise, and sensory  
61 feedback. In this formulation, motor commands were chosen to achieve task goals based on an estimate of  
62 state that combined sensory feedback with the system's prediction of the current state. The task goals are  
63 represented as a cost-to-go function. The cost-to-go function ascribes the current state a value that  
64 combines how well it leads to achievement of task goals and how much effort will be required to achieve  
65 them. Reza Shadmehr and John Krakauer (2008) used Todorov's optimal feedback control framework as

66 the basis for a computational neuroanatomy of motor control. In their scheme, primary- and pre-motor  
67 cortices generate motor commands, while the basal ganglia evaluate the cost-to-go function, and the  
68 cerebellum predicts upcoming state. In recent years, the term computational neuroanatomy mostly refers  
69 to algorithm-based quantitative approaches to image processing and 3D reconstruction associated with the  
70 study of neuroanatomy. Here we use it in the same sense used by Shadmehr and Krakauer (2008) to  
71 describe the identification of distinct motor control processes from computational models and their  
72 mapping to different brain regions.

73 In this paper, we try to extend these influential theories in two key ways. First, we suggest that  
74 each of the cortical areas involved in motor control may be implementing the model described by  
75 Shadmehr and Krakauer (2008), based on anatomical evidence that each cortical region forms its own  
76 loops with the basal ganglia and the cerebellum. Second, we suggest that these different cortical areas may  
77 be interacting in ways that are consistent with existing influential perspectives on the cortical hierarchy,  
78 that focus on the cortex's role in representing prediction and optimal information utilization (Clark, 2013;  
79 Kanai et al., 2015). These two extensions combine to produce a new, coherent model of the neuroanatomy  
80 of motor control.

### 81 **Multiple cortical loops with the basal ganglia and the cerebellum**

82 Compelling anatomical evidence supports the existence of parallel loops connecting cortical areas  
83 with both the basal ganglia and cerebellum. The loops are characterized by a high degree of topographic  
84 specificity (Middleton and Strick, 1997, 2001). Most areas of cortex receive input from dedicated, separate  
85 regions of the basal ganglia, and the most prominent input to a given region of the basal ganglia derives  
86 from the same area of cerebral cortex to which it projects. Most cortical areas have a similar loop with  
87 cerebellum (Bostan and Strick, 2018; Dum and Strick, 2003; Kelly and Strick, 2003; Middleton and Strick,  
88 1997). Neuroanatomical studies have demonstrated that cerebellar output reaches many areas of the cortex,  
89 including the posterior parietal cortex and regions of prefrontal cortex (see Bostan et al., 2013, for review).  
90 The primary somatosensory cortex has projections to the basal ganglia (Kunzle, 1977) and the cerebellum  
91 (Middleton and Strick, 1998). Gerbella et al., (2016) suggested that cortical regions connected one to  
92 another (such as specific sectors of the premotor and parietal cortex) also have convergent projections to  
93 the same striatal sectors. But the figures for individual monkeys suggest that it is a group effect due to  
94 inter-subject variability in the projections, and within each monkey there is only partial overlap in the  
95 striatal sectors (e.g. case 62, Figures 10 and 11). Neuroimaging is lacking the resolution to address the  
96 different pathways, yet, human neuroimaging studies also support the notion that different cortical regions  
97 are bidirectionally connected to distinct areas of the cerebellum and the basal ganglia (Buckner et al., 2011;  
98 Choi et al., 2012; O'Reilly et al., 2010; Seitzman et al., 2020; Yeo et al., 2011).

99 A model based on this notion of parallel segregated loops of different cortical areas with the basal  
100 ganglia and the cerebellum was first presented by James Houk, who refers to it as a distributed processing

101 module (DPM) (Houk, 2001, 2005; Houk et al., 2007). According to Houk, a given area of cortex together  
102 with its subcortical loop(s) forms a DPM and the different distributed modules communicate with each  
103 other through cortico-cortical connections. Cognitive neuroscientist Takashi Hanakawa suggested a model  
104 similar to the DPM model to explain how the premotor cortex can serve as a gateway between motor and  
105 cognitive networks (Hanakawa, 2011). The Hanakawa model is consistent with the model we present  
106 below, although our focus is on the roles of premotor and parietal cortices in task-body integration where  
107 the Hanakawa model focuses on motor–cognitive integration.

108         Recent findings of direct connections between the basal ganglia and the cerebellum (Bostan and  
109 Strick, 2018; Quartarone et al., 2020) adds complexity to the view of parallel segregated loops. However,  
110 one prominent theory proposes that the newly found connections are part of an integrated network which  
111 balances the relative influence of the basal ganglia and the cerebellum without changing their respective  
112 roles (Bostan and Strick, 2018; Taylor and Ivry, 2014). More controversially, there are recent reports of  
113 actual reward processing in the cerebellum (Medina, 2019) based on findings of reward signals in  
114 cerebellar climbing fibers (Heffley et al., 2018; Kostadinov et al., 2019). This may challenge the canonical  
115 view of the cerebellar role in motor control and learning. However, it is also possible that the reward  
116 signals reflect upstream influences of reward on kinematics (Lixenberg et al., 2020). Another suggestion  
117 is that some climbing fibers play a homeostatic role and do not affect motor learning (Tang et al., 2017).  
118 A final alternative is that reward signals in the cerebellum are found more laterally in the cerebellum and  
119 thus reflect internal modelling of reward that is not directly connected to movement (Heffley and Hull,  
120 2019; Sendhilnathan et al., 2020; Tsutsumi et al., 2019). Considering other recent results showing that  
121 climbing fibers provide predictive signals about movement parameters (Streng et al., 2018) the canonical  
122 view is still widely accepted (Apps et al., 2018; Sokolov et al., 2017).

123         It is also worth considering recent findings suggesting that basal ganglionic dopamine signals do  
124 not necessarily reflect reward prediction error (Cox and Witten, 2019). These findings are in line with an  
125 increasingly prominent hypothesis that direct and indirect pathways in the basal ganglia circuit  
126 respectively calculate parallel and separate evaluations of action selection and outcome evaluation  
127 (Nonomura et al., 2018; Stephenson-Jones et al., 2013, 2016). This would explain why neurons associated  
128 the direct pathway would not be sensitive to reward. This hypothesis is consistent with findings that the  
129 activity of substantia nigra dopaminergic neurons not associated with reward is strongly associated with  
130 movement selection and movement vigor (Da Silva et al., 2018).

## 131 **Cortical function**

132         The cerebral cortex has a laminar organization, and certain aspects of the laminar organization are  
133 preserved across most of cortex. This includes many aspects of the distribution of neurons appearing in  
134 each layer; it includes aspects of the structure of interlaminar connections; it also includes the layers  
135 producing local and projection efferents (Shipp, 2007). The similarity in the connectivity patterns of the

136 cortical layers, as well as the patterns of input and output from thalamus and other subcortical structures,  
137 has long been taken to imply that different cortical areas employ similar cortical algorithms (Douglas and  
138 Martin, 2004; Mumford, 1991, 1992), and that the cerebral cortex, like the cerebellum and basal ganglia,  
139 is specialized for a particular computation that is applied in different contexts (Doya, 1999).

140 However, recent findings highlighting the heterogeneity across cortical areas mean that the  
141 computation performed may vary with the context (Palomero-Gallagher and Zilles, 2019). The variability  
142 in the neurochemistry of the different cortical areas and the variation in the width of the different cortical  
143 layers (Zilles and Amunts, 2010), as well as the variability of the patterns of lateral connectivity (Sirosh  
144 et al., 1996) suggest that the cortical algorithm varies in ways that match specific processing demands in  
145 each area of cortex (Barbas, 2015). To take a familiar example, the target of thalamic input, layer IV, is  
146 unusually thick in visual cortex. This makes sense, since this input brings the visual input to visual cortex.  
147 In contrast, layer IV is non-existent in the motor cortex. Thalamic input to motor cortex, which represents  
148 the output of the basal ganglia and the cerebellum, projects to other layers. Thus, processing in the two  
149 areas will be different despite the many similarities between them.

150 One traditional view of the cortical structure is that the cortex is essentially a tool for  
151 representation: each area of cortex represents different aspects of reality based on the inputs it receives  
152 and the sensory-motor receptive fields of its neurons (Penfield and Boldrey, 1937). Thus, information from  
153 various sensory receptors flows forward and accumulates progressively to create a full picture of the real-  
154 world scene (Marr, 1982). A more recent view looks at the brain as a dynamical system. The dynamical  
155 systems perspective predicts that “the evolution of neural activity should be best captured not in terms of  
156 movement parameter evolution, but in terms of the dynamical rules by which the current state causes the  
157 next state” (Shenoy et al., 2013). While some find this view to explicitly contrast with a representational  
158 view, it can also be viewed as a framework of constraints on neural representations and their dynamics  
159 (Churchland et al., 2010). Under this logic, even if we accept the representational view, the representations  
160 must be structured so that their dynamics interact meaningfully with the dynamics of the real world being  
161 represented (Churchland et al., 2010, 2012; Michaels et al., 2016). Structural and neurochemical variations  
162 between cortical regions may reflect differences in the aspects of reality being represented (Palomero-  
163 Gallagher and Zilles, 2019). These differences would certainly include differences in the time constants  
164 of the dynamics as well as the relative importance of prediction and reliability of new information. It may  
165 also reflect the dimensionality of the predictive space.

166 Karl Friston and colleagues have been developing a related approach suggesting that cortical  
167 representation is essentially predictive (e.g., Bastos et al., 2012; Clark, 2013; Friston, 2010; Kanai et al.,  
168 2015). In this view, cortex mimics the dynamics of the represented world in order to represent future  
169 sensory stimulation. In their view, motor commands are characterized as predictive representations of  
170 proprioceptive input (Adams et al., 2015). Importantly, parallel segregated loops are a key property of the  
171 canonical circuits for predictive coding suggested by Friston and colleagues (Bastos et al., 2012).

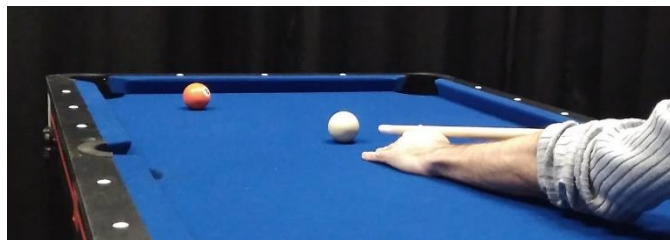
172 Incorporating the dynamical and predictive accounts of cortical function and the parallel loops described  
173 above into the Shadmehr and Krakauer (2008) scheme leads to a multi-layer model described in the next  
174 section.

## 175 **A revised model for neuroanatomy of motor control**

176 Here we consider the different aspects of reality that might be dynamically represented in different  
177 cortical areas. We address two orthogonal dissociations: body vs task and state vs action. What the body  
178 is actually doing we call body-state. Our motor commands and our active efforts to move the body we call  
179 body-action. Similarly, task-state and task-action represent the movement within the task space. Let us  
180 consider again the example of driving discussed earlier. In this situation, body-state is the configuration of  
181 our body (hands resting on the wheel, right foot pressing the gas pedal) while body-action is the movement  
182 of our limbs (moving the hands to rotate the steering wheel and changing the pressure applied by the foot  
183 to the pedals). Task-state is the configuration of the car within the task (the car is driving 60 mph in the  
184 right lane), and task-action is the movement of the car within the task (taking a turn, accelerating, or  
185 breaking).

186 In many situations, these different predictive dynamical representations are highly correlated.  
187 When we reach to a visual target, task-state encodes origin, target, and cursor position; task-action is the  
188 movement of the cursor to the target; body-action is the movement of the hand. In the absence of  
189 “experimenter trickery” (such as the well-studied visuomotor perturbations), these naturally represent the  
190 same direction. Neuronal coding might be quite similar in different cortical areas (e.g. cells with similar  
191 directional tuning (Mahan and Georgopoulos, 2013)). This connects to the familiar credit assignment  
192 problem (Wolpert and Landy, 2012), as an error can be assigned to different representations of the body  
193 and the task. The system relies on various cues, priors and heuristics to resolve the source of its errors  
194 (Berniker and Kording, 2008; Wei and Körding, 2009), although the computational details are still being  
195 explored (Gaffin-Cahn et al., 2019; McDougle et al., 2016; Parvin et al., 2018).

196 The differences between the different  
197 representations become clearer in the context  
198 of a more complex task. For instance, we  
199 consider pool or billiards (Haar and Faisal,  
200 2020; Haar et al., 2019). In preparing and  
201 making a shot (Figure 1), task-state encodes  
202 ball locations and movement and the pocket  
203 into which you want to sink the ball. Task-  
204 action is defined on the table: how the cue stick  
205 hits the white ball and the effect it should have

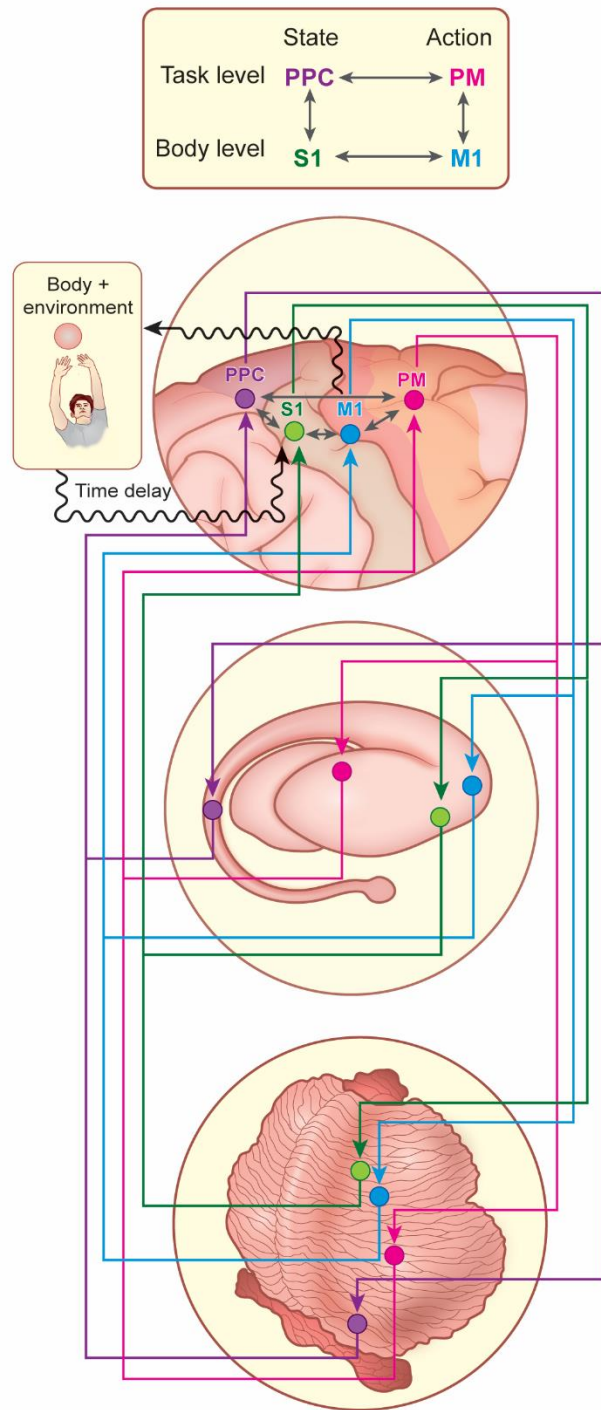


**Figure 1.** A game of billiards as a model for state and action representations. The task-state would encode mostly the locations of the white ball, the red (target) ball, and the pocket which you want to sink the ball to. The task-action would be the action on the table – the cue stick should hit the white ball in a certain position with a certain angle, spin, and speed, and the white ball should hit the target ball and push it towards the pocket. The body-state would be the player's posture and the way he/she holds the cue stick; and the body-action would be the movement that he/she does to move the cue stick.

206 and how the white ball should hit the target ball to push it towards the pocket. In contrast, body-state  
 207 describes your posture and the way you are holding the cue stick while body-action is the movement you  
 208 make to take the shot.

209 Our model combines Houk's DPM model  
 210 with Shadmehr and Krakauer's scheme based on  
 211 optimal control theory. That is, we propose a  
 212 multi-layer model where at the center of each  
 213 layer is a cortical region. For each cortical region,  
 214 activity is affected by a loop through the basal  
 215 ganglia that incorporates expected costs and  
 216 rewards into its dynamics. The dynamics of each  
 217 region is also affected through connections with  
 218 an area of the cerebellum that does predictive  
 219 error correction: it predicts and corrects persistent  
 220 errors in the cortical representation of dynamics.  
 221 This is consistent with the suggestion by Donchin  
 222 and Frens (2009) that state estimation is actually  
 223 computed in the deep cerebellar nuclei, and with  
 224 the findings of Gao et al., (2018) showing that  
 225 ongoing movement representation in the cortex is  
 226 dependent on the cerebellum. Together, the  
 227 different cortical regions represent a predictive  
 228 representation of both state and action (Figure 2).

229 This view fits naturally with the proposal  
 230 that cortex is a tool for predictive estimation and  
 231 dynamic representation. It elaborates the proposal  
 232 by suggesting that what distinguishes the different  
 233 areas of cortex is that they emphasize different  
 234 parts of reality with different dynamics. For the  
 235 motor system, we propose that premotor, primary  
 236 motor, somatosensory and posterior parietal  
 237 cortices all predictively represent the ongoing  
 238 reality and dynamics of our motor behavior but  
 239 with different emphases. We hypothesize that  
 240 primary motor cortex (M1) and primary  
 241 somatosensory cortex (S1) are concerned with the



**Figure 2.** A multi-layer model for motor control. In each layer (marked by different colored dots and arrows), a cortical region is making a loop with a designated area in the basal ganglia for expected costs and rewards, and another loop with an area of the cerebellum for forward modeling and state estimation. Each layer represents different function over the two fundamental divisions of task vs body and state vs action. Bi-directional communication between these different layers takes place in the cortex.

242 bodily aspects of movement where premotor cortex (PM) and posterior parietal cortex (PPC) emphasize  
 243 movement inside the construct of our current task. At the same time, the frontal areas (M1 and PM) are  
 244 associated more strongly with action for both body and task while the parietal areas (S1 and PPC) are  
 245 concerned with body-state or task-state. The idea that M1, S1, PM and PPC have differential functions in  
 246 body state and task conditions was suggested before (Cisek and Kalaska, 2010), but using different terms  
 247 and not in the framework of optimal control.

248 In our model, activity in M1 and PM determines eventual motor output, and the interactions  
 249 between them creates body-action and task-action chosen in concert. The activity in these areas at any time  
 250 is determined in part by the ongoing dynamics of task and body actions. However, it is also influenced by  
 251 the current state of the task and the body, and these are predicted by parietal cortex. All of these dynamics  
 252 must be shaped with the aim of achieving task goals. Parietal cortex must ensure that predictions of body-  
 253 state reflect known dynamics of the body and ongoing sensory input. It must also ensure that predictions  
 254 are updated in concert with predictions of task-state. Predictions of task-state must reflect known task  
 255 dynamics.

256 Mathematically, our model is based on that of Shadmehr and Krakauer (2008) but extends its  
 257 dimensionality. That is, for Shadmehr and Krakauer, there was only one cortical / subcortical loop while  
 258 our model considers multiple loops. This means that our definitions of state must be expanded to reflect  
 259 the state in each of the loops simultaneously and the interactions between them. Thus, superficially, the  
 260 ‘‘internal model’’ of the dynamics as a linear function of motor commands is the same:

$$\hat{x}^{(t+1|t)} = A\hat{x}^{(t|t)} + Bu^{(t)} \quad (1)$$

$$\hat{y}^{(t)} = \hat{H}\hat{x}^{(t)} \quad (2)$$

261 where  $u^{(t)}$  is the motor command, and  $\hat{y}^{(t)}$  is the expected sensory consequence.  $\hat{x}^{(t|t)}$  represents the  
 262 predicted state at time t given current and previous sensory feedback. However, in our model the  
 263 dimensionality of the state vector is increased to include the hypothesized states of the different cortical  
 264 representations:

$$\hat{x} = \begin{pmatrix} x_{BA} \\ x_{TA} \\ x_{BS} \\ x_{TS} \end{pmatrix} \quad \begin{array}{l} BA = \textit{Body Action} \\ TA = \textit{Task Action} \\ BS = \textit{Body State} \\ TS = \textit{Task State} \end{array} \quad (3)$$

265 The body-action and task-action here are not the descending motor command  $u$  but the cortical  
 266 representations of action in the body space and in the task space, which play a role in determining  $u$ , but  
 267 are distinct from it and are also influenced by dynamics of the entire system. Matrix A represents the  
 268 dynamics of the state. Its block diagonal reflects the dynamics of each cortex separately while the off-  
 269 diagonal blocks describe the cortico-cortical interactions:



$$A = \begin{pmatrix} A_{BA} & D_{BA \leftarrow TA} & D_{BA \leftarrow TS} & 0 \\ D_{TA \leftarrow BA} & A_{TA} & 0 & D_{TA \leftarrow TS} \\ D_{BS \leftarrow BA} & 0 & A_{BS} & D_{BS \leftarrow TS} \\ 0 & D_{TS \leftarrow TA} & D_{TS \leftarrow BS} & A_{TS} \end{pmatrix} \quad (4)$$

270 The single motor command  $u$  influences each cortical representation differently and B captures these  
271 different effects:

$$B = \begin{pmatrix} B_{BA} \\ B_{TA} \\ B_{BS} \\ B_{TS} \end{pmatrix} \quad (5)$$

272 Again, as reality is unified, the state of the different cortical areas must be combined to generate a single  
273 sensory vector of sensory predictions,  $\hat{y}$ . For simplicity, we take the sensory feedback to only include  
274 proprioceptive and visual components,  $y = \begin{pmatrix} y_p \\ y_v \end{pmatrix}$ , though, in principle it probably also affects other  
275 modalities including auditory and haptic. The relative contributions of the different cortices to the  
276 prediction of sensory feedback is determined by the matrix H in equation 2:

$$H = \begin{pmatrix} H_{p,BA} & H_{p,TA} & H_{p,BS} & H_{p,TS} \\ H_{v,BA} & H_{v,TA} & H_{v,BS} & H_{v,TS} \end{pmatrix} \quad (6)$$

277 In addition to equations 1 and 2 above that describe internal representation of state dynamics and input  
278 prediction, the model includes a Kalman gain equation, updating the belief state at time  $t+1$ , given the  
279 acquired sensory information. Here, again, our equation is identical to that of Shadmehr and Krakauer:

$$\hat{x}^{(t+1|t+1)} = \hat{x}^{(t+1|t)} + K^{(t+1)}(y^{(t+1)} - \hat{y}^{(t+1)}) \quad (7)$$

280 However, in our model the Kalman gain includes separate blocks from the physical dimensions of the  
281 sensory consequences to the neural diminutions:

$$K^{(t+1)} = \begin{pmatrix} K_{BA,p} & K_{BA,v} \\ K_{TA,p} & K_{TA,v} \\ K_{BS,p} & K_{BS,v} \\ K_{TS,p} & K_{TS,v} \end{pmatrix} \quad (8)$$

282 Also, in the “cost to go” function:

$$u^{(t)} = -G^{(t)}\hat{x}^{(t|t-1)} \quad (9)$$

283 the matrix G would not be in sensory dimensions (v,p) but in neural dimensions:

$$G^{(t)} = (G_{BA} \quad G_{TA} \quad G_{BS} \quad G_{TS}) \quad (10)$$

284           Importantly, the state vs action dissociation here is not simply sensory vs motor. The state  
285 representation of the body ( $x_{BS}$ ) is more than its sensory state. Even in the absence of any sensory feedback  
286 there is a representation of the current state of the body (posture, fatigue, etc.) and the future states the  
287 body can transition towards. The task-state representation ( $x_{TS}$ ) is even more distinct from a sensory  
288 representation as it accounts for all abstract rules of the task, like driving on the right or the left side of the  
289 road. Similarly, the body vs task dissociation addressed here is different than the common dissociation of  
290 intrinsic vs extrinsic coordinate frames (e.g. Buneo and Andersen, 2006; Haar et al., 2017a; Kalaska et al.,  
291 1997; Wiestler et al., 2014). In fact, both body and task can be represented in either coordinate frame or  
292 in both. Indeed, there is evidence for both intrinsic and extrinsic coordinate frames in the different cortices  
293 discussed (e.g. Wu and Hatsopoulos, 2006, 2007). Nevertheless, in the primary sensorimotor cortices those  
294 representations, in any coordinate frame, would always be of the body and not the task (e.g., the hands on  
295 the steering wheel and not the car on the road). Similarly, in the PM and the PPC those representations, in  
296 any coordinate frame, would always be of the task and not the body.

297           The representations of the body's state and action are not at all independent, of course; the extent  
298 to which they interact is attested by the strong connectivity between M1 and S1 (equation 4). However,  
299 while they are both fundamentally representing the same thing – the position of the body and its movement  
300 – they represent different aspects of that same thing. M1 is focused on the world of our possible movements  
301 while S1 is focused on what effect our movements and the world around us will have on our body.  
302 Accordingly, limb perturbation should be processed first in S1 (body-state) and then in M1 (body-action)  
303 and PPC (task-state), as the change in the body-state affects both body-action and task-state. Only then  
304 will processing pass to PM (task-action), which is affected by body-action and task-state but not directly  
305 by body-state (see equation 4). Indeed, an examination of the relative timing of perturbation-related  
306 activity across sensory and motor cortices showed this timing gradient (Omrani et al., 2016). Moreover,  
307 the authors found that when the same perturbation is applied with and without task context, the earliest  
308 and the biggest difference in the neural response is in the PPC, as the task is not experimentally defined  
309 and might not be the same in all trials. Thus, the same change in body-state does not induce a consistent  
310 change in task-state.

311           In our daily behavior, we do not generally tend to think about or understand our movements in  
312 terms of our body and our bodily motor commands. We do not make aware decision which muscle to flex  
313 and which to extend in order to move our hand. Nearly every movement is part of a motor task and we are  
314 controlling our performance in that task in order to achieve certain task goals. While driving, we think  
315 about turning the car left, not about the way our hands rotate the steering wheel. In the billiards example,  
316 we think about hitting the ball and creating its trajectory. We do not focus on the flexion or abduction of  
317 our shoulder and elbow. While in many experimental paradigms, body-state and task-state are identical,  
318 they are often not identical in real life. In addition to the examples above, one may consider video games,  
319 riding a bike, driving or typing as situations where body-state and task-state are dissociated. Similarly,

320 what constitutes a desirable, rewarding body-state may be quite different, on its face, than a desirable  
321 rewarding task-state. I may well bring my body into uncomfortable or unstable positions to achieve task  
322 goals.

323         These fundamental distinctions between body-state and task-state and between body-state and  
324 body-action can be extended to similar distinctions between task-action and body-action and between task-  
325 action and task-state. The essential point is that each of the representations has a different natural dynamics  
326 (what is most likely to come after what), a different set of goals and rewards (what is comfortable and  
327 what is effortful) and a different collection of complexities and non-linearities that may be hard to capture.  
328 One important consequence of this idea of multiple representation of different aspects of the situation is  
329 that it emphasizes the importance of bidirectional communication between them (Clark, 2013). A  
330 reasonable prediction about task-state is informed by task-actions. That is  $D_{TA \leftarrow TS}$  in Matrix A (Equation  
331 4). Task-actions then affect task-state ( $D_{TS \leftarrow TA}$ ). Body-actions must, in turn, realize the chosen task-  
332 actions. However, task-actions cannot be chosen without considering the feasibility of associated body-  
333 actions. Reality itself is multi-level and hierarchical, and, cortex must reflect this underlying structure to  
334 successfully model it. The mapping between the different representations cannot be pre-specified but must  
335 be learned. Thus, in the driving example, a novice driver has no natural map between foot presses and car  
336 dynamics. Therefore, driving instructors need an instructor's brake pedal. The novice driver needs to learn  
337 the parameters for the task / body dependencies (D parameters in the dynamics matrix in eq. 4).

338         As discussed, Hanakawa (2011) presented a model, similar to ours, describing the role of pre-  
339 motor cortex in mediating between motor and prefrontal-cognitive cortices. Under the combined  
340 framework, we can imagine that prefrontal cortex could represent our ongoing plans, strategies and desires.  
341 These should guide the task-action which later guide the body-action. Caminiti et al. (2017) also emphasize  
342 the importance of task-related processing in higher level areas but focus on the relationship of the task /  
343 body system with higher order processing of reward, motivation, and attention in ways that are reminiscent  
344 of Hanakawa's model, but do not focus on the relative role of motor and premotor cortices.

345         In our model, each of the different cortical areas has projections to the basal ganglia to account  
346 for the different costs and rewards associated with each type of representation. In essence, it follows the  
347 model of Nakahara et al., (2001) which suggests that parallel cortico-basal ganglia loops learn different  
348 coordinates with different costs and rewards. We suggest those are not coordinates but representations of  
349 task vs body and state vs action. For instance, Yeo et al., (2016), discuss the fact that one consequence of  
350 movement is its effect on the quality of sensory information. They show the need to account for sensory  
351 costs in the framework of optimal feedback control. Following this logic, basal ganglia interactions with  
352 sensory cortices may relate to optimizing our behavior to maximize the relevant sensory precision.

353         Inherent in this perspective is an approach to simultaneous representation of state and action. Since  
354 each cortical area is representing a particular aspect of reality, inherent in that representation is the implied

355 representation of the dynamics of that aspect of reality. That is, a state representation contains in it,  
356 necessarily, an understanding of which states can arise from which other states. In addition, the dynamics  
357 of state are influenced by ongoing action so that the pre-central areas must influence the post-central state  
358 representations. Similarly, a central part of action representation is the way that one action flows into the  
359 next (or leads to the holding of a posture). The dynamics of movement are just as much informed by the  
360 ongoing dynamics of state as ongoing state dynamics are informed by knowledge of ongoing actions.

361 Generally speaking, the dynamics of both body and task are high-dimensional, non-linear, and  
362 changing over time. Thus, generally speaking, the predictive representations of every cortical area will be  
363 fraught with error. In this sense, if the cerebellum engages in error-driven learning, it can serve each of the  
364 cortical areas by learning to predict the errors in its predictive representation. This is precisely the  
365 interaction between cerebellum and cortex hypothesized by Doya (2000). In this view, the cerebellum will  
366 play a different role when it corrects for the errors in different cortical representations. However, although  
367 the form of the errors will depend on the domain being represented and the model that has developed, the  
368 computations underlying the cerebellar circuitry will be the same.

## 369 **Task representations**

370 The proposed roles of M1 and S1 in representing body-action and body-state, respectively, are  
371 straightforward. We use new terminology to describe the commonly accepted roles of these areas. As such,  
372 we do not need to take a position on classical debates regarding coordinate systems (muscles versus  
373 movements). From our perspective, this is a discussion of how body-action is encoded: important in itself  
374 but at a level of description that is not our focus. The roles of the posterior parietal cortex and the premotor  
375 cortex in task-state and task-action representation, respectively, require further discussion. There is much  
376 less clarity about their roles and more work needs to be done to show how our perspective fits in with  
377 previous ideas. In the next section, we demonstrate how our perspective helps make sense of the literature.

## 378 **Posterior parietal cortex represents task-state**

379 There are several schools of thought about the role of posterior parietal cortex. One common view  
380 is that the PPC serves as a sensorimotor interface for visually guided movements (e.g. Buneo and  
381 Andersen, 2006). As such it is involved mostly in sensory-motor mapping and motor planning (Andersen  
382 and Buneo, 2002; Cohen and Andersen, 2002). Perhaps the leading alternative view is that the PPC is a  
383 state estimator, as was originally suggested by Daniel Wolpert and colleagues (Wolpert and Ghahramani,  
384 2000; Wolpert et al., 1998) and later integrated into the current model of computational neuroanatomy for  
385 motor control (Shadmehr and Krakauer, 2008). Other possibilities have also been put forward. They  
386 include high-order sensory-motor information integration in support of high-level motor functions (e.g.  
387 Fogassi and Luppino, 2005), and conscious motor intentions (e.g. Desmurget and Sirigu, 2012). We

388 believe that thinking in the abstracted terms of task-state representation will help clarify this extensive  
389 literature and subsume alternative perspectives within a single framework.

390 Grea et al., (2002) reported that a patient with bilateral posterior parietal cortex damage had no  
391 difficulty reaching to targets in their central fixation, but when the target jumped at reach onset the subject  
392 could not correct for it and continued to reach to the original target location. Desmurget et al., (1999)  
393 produce similar results on healthy subjects using a single pulse transcranial magnetic stimulation at reach  
394 onset. This phenomenon is a classic example for a deficit in task-state representation. The subject simply  
395 could not adjust to the sudden change in the task-state. A study by Funamizu et al., (2016) produced similar  
396 results using optogenetics in mice. Mice express learning in a task by increased anticipatory licking as they  
397 approached their goal, even in the absence of external cues. Thus, the mice are expressing their estimation  
398 of task-state. The authors showed that silencing of PPC prevented this ability to evaluate task-state. When  
399 the PPC is intact, it encodes task-state continuously, for example, it encodes changing target position even  
400 while the body is not yet moving (Reid and Dessing, 2018).

401 It is also possible to point to works where PPC seems to be engaged in behavior that cannot be  
402 explained as either sensorimotor mapping or state estimation. In these cases, dynamical task-state  
403 representation provides a better explanation of PPC function. Fogassi et al., (2005) found that parietal  
404 neurons coding a specific behavior, show different activity when this behavior is part of different tasks.  
405 Gail and Andersen (2006) found that parietal neurons represent the task-rule (pro- or anti-reach) before  
406 any specific movement cues, indicating abstract task representation in PPC that goes beyond spatial or  
407 motor goal representations. This task-rule is a component of task-state. Hwang and Andersen (2012)  
408 showed clear differences in PPC LFPs in reaching tasks with direct and symbolic target presentation. They  
409 saw even more striking differences between visually-guided and memory-guided reaching tasks (Hwang  
410 and Andersen, 2011). Bremner and Andersen (2014) found that parietal area 5d switches its coding after  
411 target presentation so that it always codes the most relevant information for the task. Hawkins et al., (2013)  
412 showed that parietal neurons tend to be significantly tuned either during one task or during another but  
413 rarely during both. Hawkins and colleagues even interpret their results in terms of task representation  
414 suggesting that "the superior parietal lobule plays an important role in processing information about the  
415 nonstandard nature of a task". In a recent fMRI study (Heed et al., 2018), a tactile stimulation was applied  
416 to the subjects' feet while their legs were either straight or crossed. After a delay, subjects were instructed  
417 to do pro/anti-pointing towards their feet. The results show that during touch localization S1 encodes the  
418 anatomical side of the tactile stimulus while the PPC encodes it in external space. During movement  
419 planning only the PPC encodes the task rule (pro vs anti pointing). These results suggest that body and  
420 task state are dissociated in the parietal cortex.

421 Explicit visuomotor adaptation is an example where change in task-state can be isolated. In  
422 visuomotor rotation adaptation tasks, visual target and hand target become dissociated. To correct for this,  
423 subjects need to learn to move their hand away from the target, at an angle equal to the rotation angle, in

424 order to get the cursor to the target. Recent studies dissociated explicit and implicit processes in the  
425 visuomotor adaptation (e.g. Bromberg et al., 2019; Hegele and Heuer, 2010; Mazzoni and Krakauer, 2006;  
426 Taylor and Ivry, 2011; Taylor et al., 2014; Werner et al., 2015). While implicit learning (unaware error  
427 correction) should change in the task-action representation to be the cursor direction, instead of the hand  
428 direction, if the learning is explicit (aware re-aiming, the subject is aware of the perturbation and changes  
429 the movement strategy to account for the perturbation), the task-action representation should stay loyal to  
430 the hand direction and only the task-state representation and its relation to the task-action should adapt.  
431 Indeed, we found that directional selectivity in the PPC changes following visuomotor rotation adaptation  
432 (Haar et al., 2015), while directional selectivity in the primary-motor, premotor and primary-  
433 somatosensory cortex stays loyal to the hand movement direction. The rotation angle in this study was 45°  
434 while implicit adaptation to visuomotor rotation tends to be limited to about 15° (e.g. Bond and Taylor,  
435 2015; Morehead et al., 2017), suggesting that the adaptation here was mostly explicit. The small  
436 aftereffects, following the removal of the perturbation, confirm that learning was mostly explicit.  
437 Following washout, the task-state is returned to its original representation; as a consequence, the  
438 directional selectivity in the PPC also returns to its original pattern. These results were predicted earlier  
439 based on theoretical considerations (Tanaka et al., 2009).

440 Task-state representation requires high level effector-invariant components in the neural responses  
441 during hand and arm movements for general task properties like the task goal or task rule (e.g., pro- vs.  
442 anti-reach, or reach vs. grasp). This invariance in the representation of task properties will be matched by  
443 a lack of sensitivity to kinematic components that are not related to the task. On the other hand, body-  
444 action and body-state representations should reflect kinematics. Task-action representations might include  
445 both kinematic and effector invariant properties, and kinematic and effector dependent properties. Indeed,  
446 effector-invariant representation of reach vs. grasp was found in the PPC and PM but not in M1 and S1  
447 (Gallivan et al., 2013). At the same time, effector-invariant representation of reaching movement direction  
448 (in joint coordinates) was found in M1, S1 and PM, but not in the PPC (Haar et al., 2017a). The study of  
449 motor variability also supports this framework. In measurements made without feedback, where movement  
450 variability is dominated by planning noise (Dhawale et al., 2017), we demonstrated that individual  
451 movement variability magnitudes are best predicted by cortical neural variability in the PPC (Haar et al.,  
452 2017b). Thus, the variability in the PPC is variability in the task-state domain.

453 Since most motor control experimental paradigms involve visual feedback, many of the examples  
454 above could also be explained simply as if PPC is representing the visual feedback in the task. Yet, there  
455 are examples like Funamizu et al., (2016), where mice are expressing their estimation of task-state in the  
456 absence of external cues but silencing of PPC prevented this ability, which support the idea that PPC is  
457 involved in task-state estimation, regardless of specific sensory input. The Heed et al., (2018) fMRI study,  
458 which was mentioned above, used tactile stimulation (and not visual), and thus provides another support.

459 Another recent review has also managed to incorporate a broad group of approaches to the PPC  
460 within a consistent framework (Medendorp and Heed, 2019). They argue that different areas of the PPC  
461 show different behavior because they represent the world along two key axes. The first – the rostro-caudal  
462 axis – separates representation of body from that of the environment. The second – the medio-lateral axis  
463 – separates representations of different “action classes.” This review, thus, addresses an aspect of PPC  
464 function explicitly outside the scope of our review: the functional subdivisions within the PPC; their work  
465 is fully complementary to our own. For instance, they emphasize that PPC activity is highly dependent on  
466 task and context and represents those aspects of body and environment that are relevant to task  
467 performance. We suggest a generalization of their approach where rostral PPC reflects the projection of  
468 the self into the task – the representation of our ability to have direct effects in the task – rather than an  
469 explicit representation of the body which is more properly the role of S1.

#### 470 **Premotor cortex represents task-action**

471 We propose that the role of the premotor cortex is to represent task-action. Only a few studies in  
472 the existing literature can speak to this question. Most often, PM is studied in tasks involving direct reach  
473 to target. In these tasks, task-action representation is simple and consistent with both task-state and body-  
474 action. Nevertheless, some studies show dissociation between body-action representation in M1 and task-  
475 action representation in PM. For instance, Schwartz et al., (2004) used a motor illusion to separate  
476 monkeys' perception of arm movements from their actual movements during figure drawing. Trajectories  
477 constructed from cortical activity of the monkeys showed that the actual movement (body-action) was  
478 represented in M1, whereas the visualized trajectories (task-action) were found in the ventral PM.

479 Another example of this dissociation, which also emphasizes the idea of the parallel loops, comes  
480 from motor adaptation studies in cerebellar patients (Donchin et al., 2012; Rabe et al., 2009). The results  
481 of these studies suggest that patients with pathology in the anterior parts of the arm representation of the  
482 cerebellum, apparently connected to M1, failed to adapt to force-field perturbation. This is presumably  
483 because force field adaptation requires adapting the relation between task-action and body-action. Patients  
484 with a lesion in a more posterior part of the arm area, apparently connected to PM, failed to adapt to  
485 visuomotor perturbation. Again, one may presume that this is because visuomotor adaptation requires  
486 changes in the relation between task-state and task-action. Recent modeling work on neural recordings  
487 from M1 and dorsal PM reached a similar conclusion: force-field adaptation changes the relationship  
488 between PM and M1; visuomotor adaptation causes changes upstream to M1 (Perich et al., 2018).

489 In stroke patients performing imitation movements, deficits were found to be associated with PM  
490 lesions. Imitations were equally impaired when cued by actor's arm movement or by a cursor, suggesting  
491 abstract body-independent movement representation (task-action) in PM (Wong et al., 2019). Further  
492 support for this dissociation can be found in the result of a study (Saber-Moghadam et al., 2016) showing  
493 that when target jumps caused a sudden change in motor intention, this led to earlier changes in PM activity

494 than in M1. In this task, information at the task level was driving the change in motor intention so task  
495 level representation changes drive changes at the body level. We predict that tasks where the perturbation  
496 is at the body level and not the task level (for instance, a perturbation of the hand that is not reflected in  
497 the cursor) should drive changes that arise first in M1.

498 More support for task-action representation in the premotor cortex can be found in the results of  
499 Pastor-Bernier & Cisek (2011) which shows that directional tuning of neurons in PM modulated following  
500 changes in rewards associated with targets in the preferred direction of the neuron. This modulated tuning  
501 reflects a change in the task-action associated with the same task state. Pearce and Moran (2012) used a  
502 complex obstacle-avoidance task and showed that PM activity is modulated both by task demands and by  
503 the particular strategy being used. They looked at the activity of the PM neurons during trials differing  
504 both in the target direction and in the obstacle opening directions and showed that the same neurons show  
505 directional selectivity both to the target direction and to the obstacle opening direction. This dual  
506 directional selectivity is a good example for task-action representation in the premotor cortex. Finger  
507 sequencing is another task where the task and body representations differ: the task-action is the sequence  
508 while the body-action is individual finger movements. Indeed, a recent fMRI study by Yokoi et al., (2018)  
509 found that after intense practice on finger sequences, activity patterns in PM and PPC encoded the task  
510 (the different movement sequences), while the activity patterns in M1 and S1 could be fully explained by  
511 the body action/state: a linear combination of patterns for the constituent individual finger movements.

512 Last, a recent study by Martínez-Vázquez and Gail (2018) looked at the LFP directed interaction  
513 between PM and PPC during movement planning and execution. They found that during movement  
514 planning the direction of the interaction is from the PPC to the PM, and during movement execution there  
515 is a flip in the direction of the interaction which flips back after execution. These findings are again  
516 consistent with our model. During planning PM receives information from PPC regarding task-state to  
517 plan task-action. During execution, PPC receives information from PM regarding ongoing task-action to  
518 update task-state.

## 519 **Concluding remarks**

520 Shadmehr and Krakauer's proposal for a neuroanatomy for motor control (2008), presented a  
521 decade ago, highlighted the cortical loops with the basal ganglia and the cerebellum and suggested that  
522 they serve for computing costs and for system identification, respectively. We present a new model  
523 inspired by that scheme that emphasizes parallel loops connecting different cortical areas with these  
524 subcortical regions. This aspect of our model draws inspiration from Houk's DPM model (Houk, 2001)  
525 and is supported by compelling anatomical evidence (Middleton and Strick, 1997, 2001). In our model,  
526 we address the notion that each area of cortex represents reality in a different way with different emphases.  
527 We suggest that the primary somatosensory and motor cortices represent respectively the state and action  
528 of the body, while the PPC and premotor cortex represent the state and action of the task.



529           While it is largely accepted that the basal ganglia and the cerebellum form parallel segregated  
530 loops with different cortical regions, there is an alternative view of a funnel like organization from wide  
531 areas of cortex through the sub-cortical regions onto a small area of cortex (Allen and Tsukahara, 1974;  
532 Kemp and Powell, 1971). Recent findings suggest caveats to the parallel segregated loops framework  
533 (Aoki et al., 2019), but still support it. If this ongoing controversy ultimately shows that the parallel  
534 segregated loops are a poor model for basal ganglia and cerebellar connectivity to cortex, our proposed  
535 model will be undermined.

536           Ultimately, we wish to emphasize that this model is only a limited cartoon and makes no attempt  
537 to capture the full complexity of the cortical hierarchy in motor control or its subcortical connections.  
538 Some of these simplifications have been addressed above. Nevertheless, our model advances the paradigm  
539 within which we think about and study the motor cortices. It points the way forward towards a developing  
540 understanding of the task / body dimension and the need to distinguish the complex relationships of each  
541 cortical area to its subcortical support and develop a fuller understanding of each of the parallel loops.

542           In models of this sort, precise anatomical definitions of the basal ganglia and cerebellum are left  
543 somewhat vague. This is true for the Shadmehr and Krakauer (2008) model, for the models of Houk (2001)  
544 and Hanakawa (2011), and also for our own model. However, the basic idea is that parallel loops with the  
545 basal ganglia will include parallel instantiations of the direct pathway, the indirect pathway, and the  
546 hyperdirect pathway (Nambu et al., 2002). Similarly, in the cerebellum, the idea is that the full cerebellar  
547 microcircuit is involved where cortical input drives mossy fibers originating in the pons as well climbing  
548 fiber input originating in the inferior olive, and that the output of the circuit will be from the dentate nucleus  
549 via the thalamus (Raymond et al., 1996).

550           Indeed, this class of models further schematizes the motor system because the models generally  
551 do not address subdivisions of the premotor and posterior parietal cortices and often leave out other non-  
552 primary motor areas such as supplementary, pre-supplementary and cingulate motor areas. The idea that  
553 the entire premotor cortex or the entire posterior-parietal cortex performs a unique function is controversial  
554 (e.g., Rizzolatti et al., 2014). The models also fail to address recent findings showing direct connections  
555 of the basal ganglia to the cerebellum (Bostan and Strick, 2018; Quartarone et al., 2020) and ignores  
556 entirely the spinal cord, red nucleus, thalamus, and other subcortical motor areas. These models have,  
557 however, helped guide thinking about the inter-relations of parts of the motor system and have been an  
558 integral part of some of the most inspiring work in our field.

559           One direction for future work would be the one laid out by King et al., (2019). These authors used  
560 a battery of motor, sensory and cognitive tasks to produce a detailed map of cerebellar function. However,  
561 the tasks they selected do not allow dissociation of task level and body level aspects of the task. As a result,  
562 their data cannot be used to directly test our hypothesis. A similar study with specifically designed tasks  
563 would be an ideal test of our model. Another possibility for testing the dissociation of task and body

564 representations in PM and M1 would be the use of brain computer interfaces. Using such interfaces, we  
565 can define a task that is driven directly by activity in premotor cortex. We predict that we could ask patients  
566 to imagine doing the task with different bodily effectors and, thus, create a situation in which we can see  
567 that premotor activity is directly related to the task while M1 activity is related to the imagined movement  
568 of the body.

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