1 **Corollary Discharge for Action and Cognition**

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23 **Abstract**

24 In motor systems, a copy of the movement command known as corollary discharge is

25 broadcast to other regions of the brain to warn them of the impending movement. The

26 premise of this review is that the concept of corollary discharge may generalize in

27 revealing ways to the brain's cognitive systems. An oculomotor pathway from the

28 brainstem to frontal cortex provides a well-established example of how corollary

29 discharge is instantiated for sensorimotor processing. Building on causal evidence from

30 inactivation of the pathway, we motivate forward models as a tool for understanding the

31 contributions of corollary discharge to perception and movement. Finally, we extend the

32 definition of corollary discharge to account for signals that may be used for cognitive

33 forward models of decision-making. This framework may provide new insights into

34 signals and circuits that contribute to sequential decision processes, the breakdown of

35 which may account for some symptoms of psychiatric disorders.

36

37 **Introduction**

38 It has been proposed that higher-level cognition in primates evolved in concert with

39 goal-directed motor control (1) and rich representations of body state (2). Cognitive and

40 motor systems both rely on sensory information for learning about the structure of the

41 world, and there is extensive evidence for shared substrates between sensory,

42 cognitive, and motor processing down to the single neuron level (3–6). During behavior,

43 sensory-to-motor signals help to specify the brain's movement commands, but at the

44 same time reciprocal motor-to-sensory signals known as *corollary discharge* relay

45 copies of the movement command to sensory areas (7). These signals keep perceptual

46   systems informed of upcoming movement plans. Given the tight linkage between

47   sensory-motor and cognitive operations, we propose that the strategy of one system

48   updating another for the purpose of coordination across processing stages may be a

49   general principle. Here we will discuss the evidence for motor corollary discharge

50   circuits in the primate brain, their function, and the extent to which *cognitive* corollary

51   discharge circuits may play analogous roles.

52   Why do we need corollary discharge? Animals need to perceive the world while

53   interacting with it, but their actions change their environment. When a monkey swings

54   through a tree, for example, the foliage rustles around her. Some of that sensory input is

55   innocuous and due to her actions, but some may represent a threat, such as a predator.

56   Disambiguation of self-generated sensory signals from environmental signals is

57   therefore fundamental to survival. Moreover, much of behavior consists of action

58   sequences made in dynamic, uncertain environments. Waiting for information about

59   where our effectors are at the end of each movement to plan the next one limits the

60   speed of graceful and accurate behavior. Predictive estimation of effector dynamics,

61   informed by corollary discharge, frees the brain from waiting for sensory confirmation of

62   each step in a sequence.

63   One way to generalize how corollary discharge aids sensory disambiguation and

64   action planning is through black box representations of system dynamics known as

65   internal models. There are two main types (8). *Inverse models* calculate the movement

66   needed to transition between a current and desired state. *Forward models* use corollary

67   discharge of movement plans, in conjunction with other information about the system, to

68   predict the sensory consequences of the movement (9, 10). The predictions can inform

69 subsequent inverse models that calculate corrective movements or the next movement

70 of an action sequence. The end result is that neural processing is more proactive and

71 less reactive, allowing for more sophisticated sensory analysis and fluid action.

72   In primates, eye movements are a useful, reduced model system for the study of

73 corollary discharge. Saccadic eye movements displace the visual image on the retina,

74 necessitating predictive mechanisms for distinguishing saccade-induced visual

75 movement from true visual object movement. Such mechanisms could include forward

76 models (11, 12). Saccades are also made in rapid sequences and thus benefit from

77 real-time monitoring of motor commands. For both of these purposes – perceptual and

78 motor – a single pathway from brainstem to frontal cortex has been shown to provide

79 corollary discharge of saccades (12–15). In this review, we use our understanding of

80 this pathway to discuss how corollary discharge operates in the primate brain. Based on

81 what we have learned from the visuo-saccadic system, we propose a definition of

82 corollary discharge that extends beyond action to include the monitoring of cognitive

83 operations. Mechanisms of corollary discharge and forward models thus may provide

84 another commonality between systems for action and cognition in the brain.

85

86 **Saccadic Corollary Discharge**

87 Evidence for a pathway that could transmit saccadic corollary discharge was found in

88 experiments that electrically stimulated the brainstem's superior colliculus (SC) during

89 recordings of neurons in the frontal eye field (FEF) of rhesus macaques. Many of the

90 FEF neurons responded as if driven via synapses from the SC (16), consistent with

91 anatomical evidence for a pathway relayed by neurons at the lateral edge of

92 mediodorsal thalamus (MD; 17). Recordings at each step of the SC-MD-FEF pathway

93 confirmed that it conveys temporal and spatial information about imminent saccades

94 (14, 18), and inactivation of the pathway caused deficits in saccadic corollary discharge

95 that affected both visual processing and motor sequencing (12, 15, 19). The pathway

96 therefore has all the characteristics expected from a corollary discharge circuit.

97   Although the focus of this review is on neural data from macaques, all of the

98 brain areas and pathways we discuss have homologs in humans. In particular, like in

99 macaques, the lateral edge of human MD thalamus contributes to saccadic corollary

100 discharge as shown by lesion studies (20–23) and connects to human FEF in

101 dorsomedial precentral sulcus of Brodmann's area 6 (24) as shown by diffusion tensor

102 imaging (25). The source of the saccadic corollary discharge is not known in humans,

103 but the SC – by all measures comparable to macaque SC (26–28) – is the most likely

104 candidate. For more on saccadic corollary discharge in humans and its relevance to

105 behavior and pathology, see the review by Thakkar and Rolfs in this volume (29).

106

107 *Source of the pathway: The SC*

108 Corollary discharge in the macaque SC-MD-FEF pathway originates in the intermediate

109 layers of the SC, where neurons generate saccadic motor commands. Electrical

110 stimulation in this region elicits saccades at extremely short latency, since only two

111 synapses intervene between it and the final motor neurons (30). The intermediate layers

112 of the SC collect information from many areas of cerebral cortex, some of which

113 combine sensory and contextual information to make a deliberate saccade plan while

114 others simply relay visual signals to trigger reflexive glances (6, 31). Integration of all

115   this information in the SC creates a signal that is more tightly linked to the impending

116   saccade than in any individual cortical area (32, 33). Corollary discharge from SC to

117   FEF is therefore the outcome of collective processing and refinement of a multitude of

118   cortically-derived, saccade-related signals (12).

119

120   *Relay node: The MD thalamus*

121   Corollary discharge from the SC projects to relay neurons at the lateral edge of MD

122   thalamus. The relay neurons, for the most part, recapitulate the signals ascending from

123   the SC (18). The population of MD relay neurons is highly concentrated, providing a

124   convenient target for reversible inactivation of the pathway (14, 15, 19). Impairment of

125   corollary discharge can be dissociated from motor impairment using the double-step

126   task, in which subjects make saccades to the remembered locations of two sequentially

127   flashed targets in the order that they appeared. To make the second saccade correctly,

128   one must monitor where the first saccade landed, information provided by corollary

129   discharge. It was shown that silencing MD spares the ability to make both saccades but

130   impairs the accuracy and precision of the second one, revealing a selective deficit of

131   corollary discharge (14, 19).

132

133   *Target of the pathway: The FEF*

134   The ascending pathway terminates in FEF layer IV. More than 90% of the neurons

135   receiving the input exhibit visual responses (16, 18), suggesting that a major role of the

136   corollary discharge is to influence visual processing. One such influence appears to be

137   the presaccadic remapping of visual receptive fields. As discovered originally in parietal

138   cortex (34) and then in FEF (35), many neurons shift their visual responsiveness just

139   *before* a saccade to the part of the visual field where their receptive field will land *after*

140   the saccade (the "future field"). Since this presaccadic remapping links visual

141   processing before and after a saccade, it is thought to contribute to the perception of

142   visual continuity across saccades (36–38). Corollary discharge in the SC-MD-FEF

143   pathway has the spatiotemporal properties needed to induce presaccadic remapping

144   (39), and reversible inactivation of the pathway reduced FEF remapping by around 50%

145   (15). In a later study, Cavanaugh et al. (13) found that inactivation of lateral MD also

146   disrupts a monkey's perception of visual stability. Rao et al. (40) trained a recurrent

147   neural network model to produce accurate arm movements to a visual stimulus despite

148   intervening saccades, as an assay for visual stability. They found that the emergence of

149   visual stability was tightly linked to that of presaccadic remapping which itself depended

150   on an intact pathway for corollary discharge. Together, these results support the

151   hypothesis that presaccadic remapping contributes to visual stability and provide

152   evidence of how disturbances to corollary discharge disrupt that stability.

153

154   **Oculomotor Forward Model: Evidence and Open Questions**

155   The role of the corollary discharge signal provided by the SC-MD-FEF pathway can be

156   formalized by placing it in the context of an oculomotor forward model (**Figure 1A and**

157   **B**) (11, 12). Justification for this depends on evidence consistent with three major

158   features of any forward model. First, the corollary discharge would need to generate

159   sensory predictions about the consequence of movement. This capability is

160   demonstrated, as discussed above, by the role of the SC-MD-FEF pathway in

161   presaccadic remapping. Neurons that remap sample, before each saccade, the part of

162   visual space that they will "see" after the saccade (12). Presaccadic remapping in the

163   FEF therefore provides a signal in visual coordinates that is appropriate for predicting

164   the consequence of each saccade (11). Analysis of microcircuitry in the FEF suggests it

165   could generate the remapping signal locally (41), and projections from the FEF could

166   relay the signals back to extrastriate cortex (42, 43) for prediction of incoming visual

167   input. Even though the FEF is the only known target of a corollary discharge pathway in

168   the saccadic system, remapping is found in earlier visual areas as well. It is prevalent in

169   the lateral intraparietal cortex (LIP; 34), V4 (44, 45), and MST (46), but diminishes lower

170   in the visual hierarchy from V3 to V2 and V1 (47, reviewed in 36). This waning of

171   remapping from higher to lower visual areas is consistent with its possible function as a

172   top-down mechanism for prediction of visual input. Presaccadic remapping has been

173   reported in human visual cortex as well (48, 49), with a similar decrease in remapping

174   from higher to lower visual areas (49).

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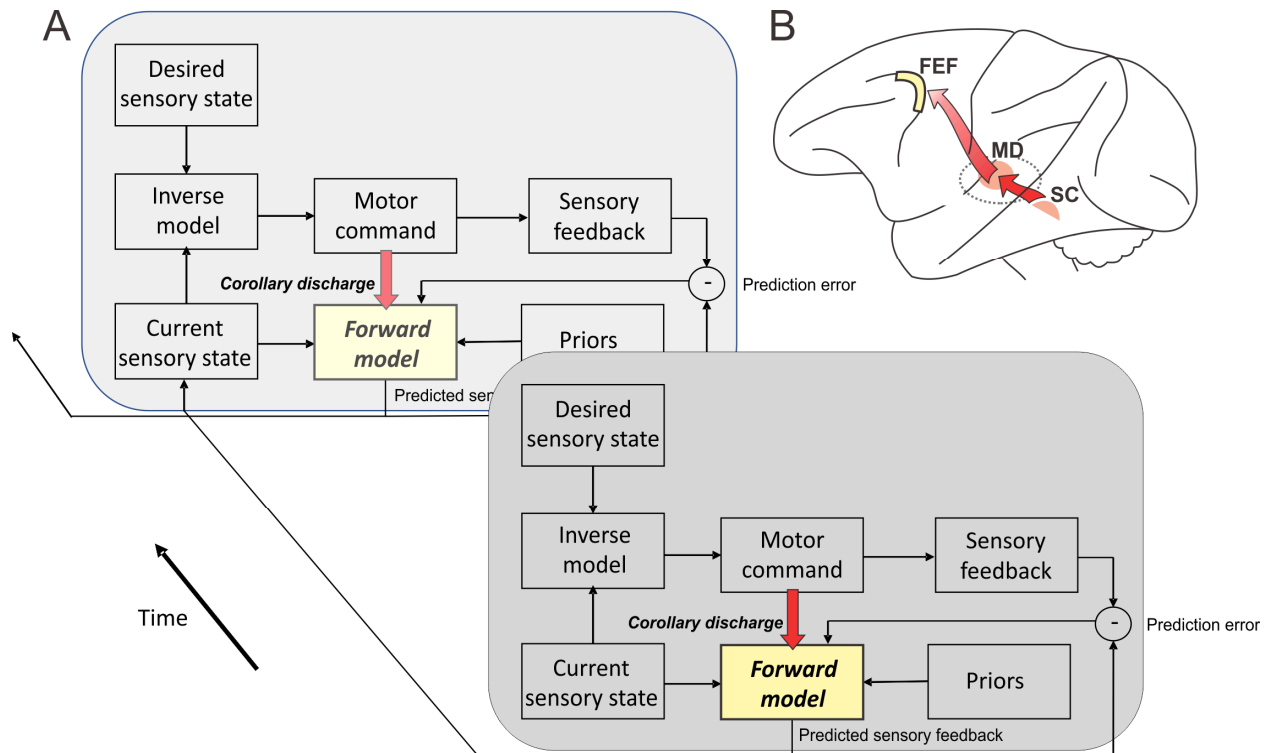
Figure 1. Sensorimotor internal models. (A) Inverse models generate motor commands to transition from a current sensory state to a desired sensory state. Forward models use corollary discharge, in conjunction with priors and the current sensory state, to predict the sensory consequence of an action. (B) In the rhesus monkey brain, as depicted, the pathway from SC to MD to FEF provides corollary discharge of saccades that may enable an oculomotor forward model.

The second feature of any forward model is that it must account for the current state of the system, in conjunction with corollary discharge, while making predictions. The current state of the system includes knowledge, or *priors,* about the effectors or the environment. A prior about effectors could be, for example, information that one of the eyes is injured, limiting the range of saccadic motion. The forward model would need to account for the gain reduction to generate accurate predictions. A prior about the

190 environment could include knowledge about objects in the world, such as their

191 propensity to move. Animals often move, for example, while rocks rarely do. Accounting

192 for the intrinsic nature of objects would improve predictions about their states across

193 saccades. Rao et al. (50) tested whether human subjects use priors in this way by

194 having them make a saccade to a visual target and report whether the target's location

195 (spatial state) changed during the saccade. Targets had varying probabilities of moving,

196 from 0.1 to 0.9, that were matched to their color. When the subjects were informed of

197 the color-probability assignments, thus instilling priors about object movement, their

198 sensitivity at detecting the state change became a function of the priors (50). This

199 indicates that the oculomotor forward model incorporates priors about the state of the

200 environment, even to the level of individual objects, when predicting the sensory

201 consequences of saccades.

202   A final component of any forward model is that the predicted sensory

203 consequence of a movement is compared with the actual sensory consequence, i.e. the

204 "reafferent" response. The difference between these signals, the prediction error, is

205 used to update future predictions. Crapse and Sommer (51) tested whether FEF

206 neurons make such comparisons about predicted versus reafferent visual responses

207 across saccades. They recorded from FEF visual neurons in monkeys that made

208 saccades to visual targets in the presence of a behaviorally-irrelevant visual probe.

209 During each saccade, the probe would stay still or move, but after the saccade it was

210 always at the center of the neuron's postsaccadic receptive field. Because the

211 postsaccadic location of the probe was constant, the null hypothesis was that reafferent

212 responses would be constant. The result, however, was that reafferent responses

213   varied as a function of how much the probe moved during the saccade. The reafferent

214   responses also were sensitive to other changes in the probe (size or color) across

215   saccades. Hence, FEF neurons exhibit a robust prediction error signal about

216   transsaccadic changes of visual stimuli.

217   Multiple lines of evidence therefore support the hypothesis that corollary

218   discharge in the SC-MD-FEF pathway contributes to an oculomotor forward model.

219   More studies are needed to test this hypothesis, integrate the individual lines of

220   evidence, and identify specific circuits and mechanisms of the forward model.

221   One way to test the oculomotor forward model hypothesis would be to check

222   whether presaccadic remapping is needed for computing the prediction error signaled

223   by FEF neurons. Is that error signal computed through a comparison of future field

224   responses and post-saccadic receptive field responses? This could be tested by

225   inactivating MD to reduce remapping in FEF (15) while examining the prediction errors

226   reported by FEF neurons (51). If the computation of prediction error signals requires

227   presaccadic remapping, it should be reduced by MD inactivation. Many other

228   mechanistic questions need to be studied, as well:

229   1) How are priors about the environment included in the feedback prediction?

230   Where are these priors represented and how do they combine with the spatial prediction

231   generated by anticipatory remapping?

232   2) How and where is the prediction error signal computed? A prediction error is

233   the difference between the feedback prediction and the incoming input. Thus, a

234   prediction error might be generated at any stage in the visual hierarchy.

235   3) How does the prediction error signal update future predictions? A prediction

236 error across a saccade could arise because of an incorrect corollary discharge signal or

237 because of incorrect information about the state of the system. Solving this credit-

238 assignment problem would require knowing the relative accuracies of each of these

239 signals and updating them accordingly. Alternatively, it is possible that the incoming

240 sensory signal itself is unreliable, which should make the prediction error less likely to

241 update one of the predictive signals. Bayesian models formalize this prediction. Within a

242 Bayesian model, the prior is equivalent to the prediction; the likelihood, the incoming

243 signal; and the posterior, the prediction error (52). Bayesian models also predict that

244 perception is closest to the posterior. A simulation study by Niemeier and colleagues

245 (53) showed that saccadic suppression is a consequence of accounting for the reliability

246 of eye movements, thus providing evidence for the implementation of a Bayesian model

247 in the oculomotor system. Whether a prior about the environment and the incoming

248 input are combined in a Bayesian manner, however, remains unknown.

249   Learning more about oculomotor forward models also could improve our

250 understanding of the circuit basis of psychiatric disorders. Eye movements are

251 abnormal in schizophrenia (54, 29 in this volume) and several of the disorder's

252 symptoms are thought to result from impairments of corollary discharge and forward

253 models (for reviews, see 55–58). In anticipation of the broader use of these concepts for

254 explaining psychiatric conditions, it seems timely to re-visit the definition of corollary

255 discharge and assess its applicability to signals within cognitive networks of the brain.

256

257 **Cognitive Forward Model: Proposal and Implications**

258 Although corollary discharge originally referred only to copies of motor commands (59),

259 that strict conception seems outdated. Even within the saccadic system, corollary

260 discharge from the SC originates at least two synapses upstream from the extraocular

261 muscles and consists of a mixture of visual responses, delay activity, and movement

262 signals (18), suggesting that corollary discharge as it exists neurally is more nuanced

263 than it was imagined theoretically. We propose that corollary discharge, broadly

264 speaking, is *any copy of a neural signal that is conveyed for informational purposes and*

265 *state updates*.

266 Consider two successive tasks, Task A and Task B, where performance of Task

267 B is contingent on Task A. These "tasks" may be any distinct operation performed by

268 the nervous system, from tapping a finger to deciding where to eat lunch. Corollary

269 discharge of Task A would be a neural signal that meets the following criteria:

270 1) It must be a copy of the command that produces Task A, in that it carries the

271 same information as the command itself.

272 2) Execution of Task A must not depend on the signal.

273 3) Execution of Task B must depend on the signal.

274 4) The signal must be produced regardless of whether Task B follows Task A.

275 The first two criteria require that corollary discharge reflects the performance of

276 Task A without causing it. The third criterion requires that the corollary discharge signal

277 be useful, in that it is needed for some Task B. The fourth criterion limits corollary

278 discharge to signals that are produced whenever Task A occurs rather than only in

279 anticipation of a specific Task B, to exclude specialized, trained signals that link the

280 tasks. In the case of saccadic corollary discharge, for example, Task A is the generation

281   of a saccade. The SC can be said to produce a corollary discharge of the task because

282   its ascending signals are 1) copies of the saccade vector, 2) irrelevant to moving the

283   eyes, 3) necessary for generating a second saccade in the double-step task and

284   remapping of visual receptive fields, and 4) obligatory.

285   Applied to neural systems that accomplish the task of decision-making, the

286   framework could help to identify *cognitive corollary discharge* signals. The plausibility of

287   such signals is suggested by a range of studies, across species, showing that when

288   individuals make decisions, they self-monitor them (60–65). The neural signals that

289   monitor decisions do not drive those decisions (66–69) but seem to provide a more

290   informational function that helps to guide subsequent decisions (70, 71). Such

291   performance-monitoring signals have the potential for meeting the criteria of a corollary

292   discharge signal in the cognitive domain.

293   In the saccadic system, corollary discharge signals inform visual processing and

294   guide the planning of subsequent saccades through putative forward models.

295   Analogously, when we say that corollary discharge of a decision may guide subsequent

296   decisions or other tasks, it implies an intermediary mechanism, which could be a

297   cognitive forward model. What would such a model look like? One well-studied type of

298   decision is made to transition from the current value state to a desired higher value

299   state. This value transition may take the form of gaining reward or avoiding punishment.

300   In this context, a cognitive forward model would generate predictions of the value

301   consequence of a decision, using a copy of the decision command (**Figure 2A**).
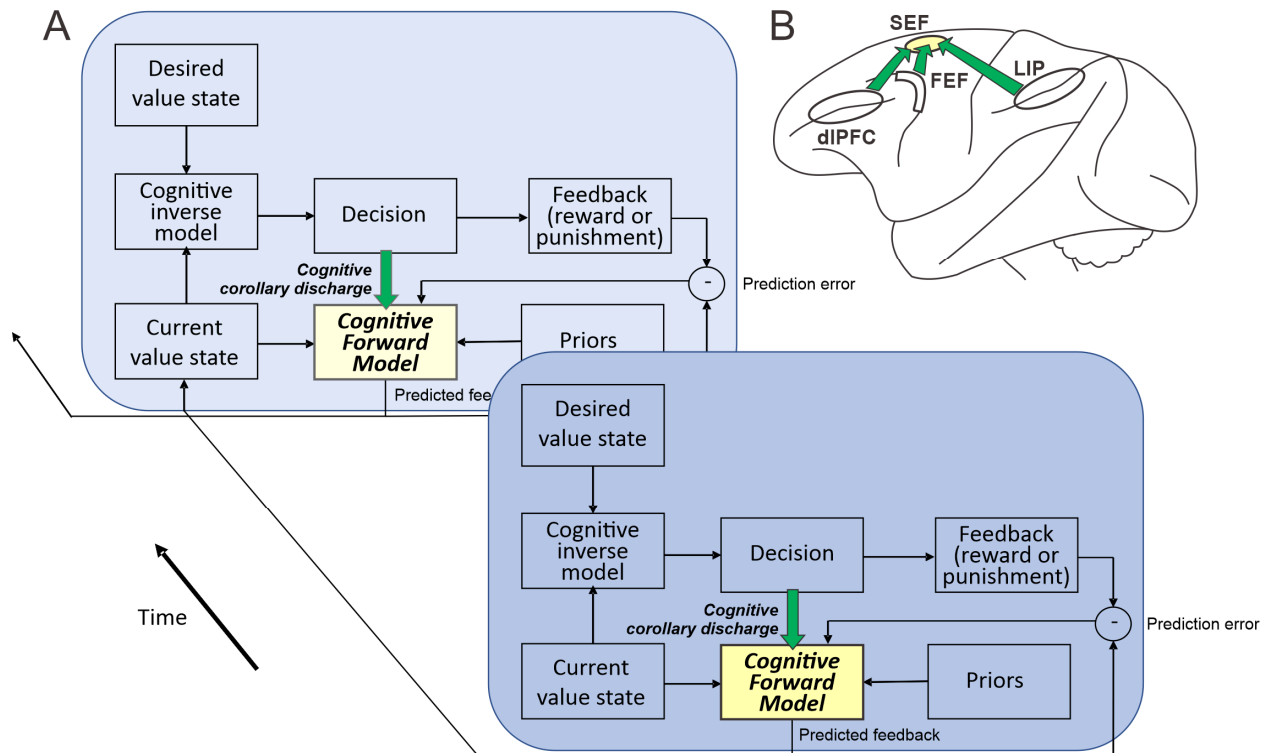
Figure 2. Cognitive internal models. (A) An example of a cognitive forward model that would use cognitive corollary discharge of decisions to predict their value consequences. (B) One candidate area for contributing to this type of cognitive forward model is the SEF. Corollary discharge of decisions could arrive from multiple possible areas including the dlPFC, the FEF, or LIP. Although depicted in the macaque brain here, all of these areas have putative homologs in the human brain: SEF in the mesial portion of Brodmann's area 6 (24, 72), dlPFC in the middle frontal gyrus portion of Brodmann's areas 9 and 46 (73, 74), FEF in dorsomedial precentral sulcus within Brodmann's area 6 (24), and LIP in Brodmann's area 7 (75).

For a forward model that mediates decision-guided value predictions, akin to motor-guided sensory predictions of an oculomotor forward model, the cognitive corollary discharge signal would enable a mapping from decision coordinates to value

316   coordinates. The model would yield a predicted value state that could be used as the

317   current value state even before reward is received, allowing decisions to be planned in

318   quick and accurate sequences. The difference between the predicted value and the

319   reinforcement that is eventually received, the prediction error, would be relayed back up

320   to local decision centers to update subsequent decisions and predictions. There is

321   widespread evidence for the existence of reward prediction and reward prediction error

322   signals across various brain areas (76–81). Indeed, reward prediction error is thought to

323   be a key driver of learning, that is, the updating of subsequent predictions to match the

324   outcome. Although there are influential computational models of how reward prediction

325   error signals might be generated (82) and some recent efforts towards investigating this

326   in neural circuits (83), we do not have a clear understanding of the components that go

327   into the calculation of reward prediction error in the brain. A cognitive forward model that

328   generates predictions about decision outcome, and in turn, prediction errors, provides a

329   plausible explanation. Cognitive forward models can be extended to include decisions

330   across sensory modalities or more abstract decisions to transition between thought

331   states. Dysfunction of these models might then explain the aberrant internal states

332   observed in many complex psychiatric disorders.

333   For decisions involving vision and eye movements, the supplementary eye field

334   (SEF) is a possible locus for the implementation of a cognitive forward model (**Figure**

335   **2B**). Simulation and inactivation studies suggest that it is not centrally involved in eye

336   movement generation (reviewed by 72), yet during visuo-saccadic tasks its neurons

337   carry signals that correspond to decision monitoring, reward prediction, received

338   reward, and reward prediction errors (68, 69, 79, 84, 85). A recent study also linked the

339   activity of neurons in the SEF to the generation of error-related negativity (ERN), an

340   electroencephalography-based measure of prediction errors (86). Abnormal ERNs in

341   schizophrenic patients are thought to reflect deficiencies in the self-monitoring of

342   thoughts and actions (87–90) and might arise from dysfunction of a cognitive forward

343   model. Such a forward model, however, cannot function without input from cognitive

344   corollary discharge, just as visual receptive fields cannot remap presaccadically without

345   information about the upcoming saccade.

346   Corollary discharge of decisions could arrive from several candidate areas

347   including dorsolateral prefrontal cortex (dlPFC) and LIP (91, 92), but a particularly

348   interesting source would be the FEF. In addition to its sensorimotor integration

349   functions, the FEF appears to contribute to sensorimotor decisions (93–96). The

350   information that the FEF receives about upcoming saccades, the visual scene, and

351   priors would be useful for both its own forward model operation and its decision-making

352   functions. Corollary discharge of the latter could inform the SEF cognitive forward model

353   (**Figure 3A**) (97), meaning that the FEF would serve as the terminus of one forward

354   model and the origin of corollary discharge for another (**Figure 3B**). This cognitive

355   corollary discharge might be relayed by a direct connection between the two regions

356   (98) or indirectly via a transthalamic pathway (99, 100, reviewed in 58). In support of the

357   latter, monkeys with lesions to MD thalamus are impaired in exploiting information about

358   their recent decisions in an adaptive decision-making task (101). Other nodes in the

359   oculomotor system, such as LIP, could provide similar interfaces between sensorimotor

360   and cognitive forward models. Neurons in LIP remap their visual receptive fields (34)

361   and carry signals both about decisions (102, 103) and the monitoring of decisions (67).

362   However, for LIP to function as a sensorimotor forward model, it would have to receive

363   saccadic corollary discharge, but no such pathway to LIP has been discovered yet.

364   Regardless, the shared neural substrate of FEF (and possibly LIP and other areas), via

365   their joint roles in forward models, might provide a direct mechanism by which cognitive

366   processing builds on sensorimotor integration.
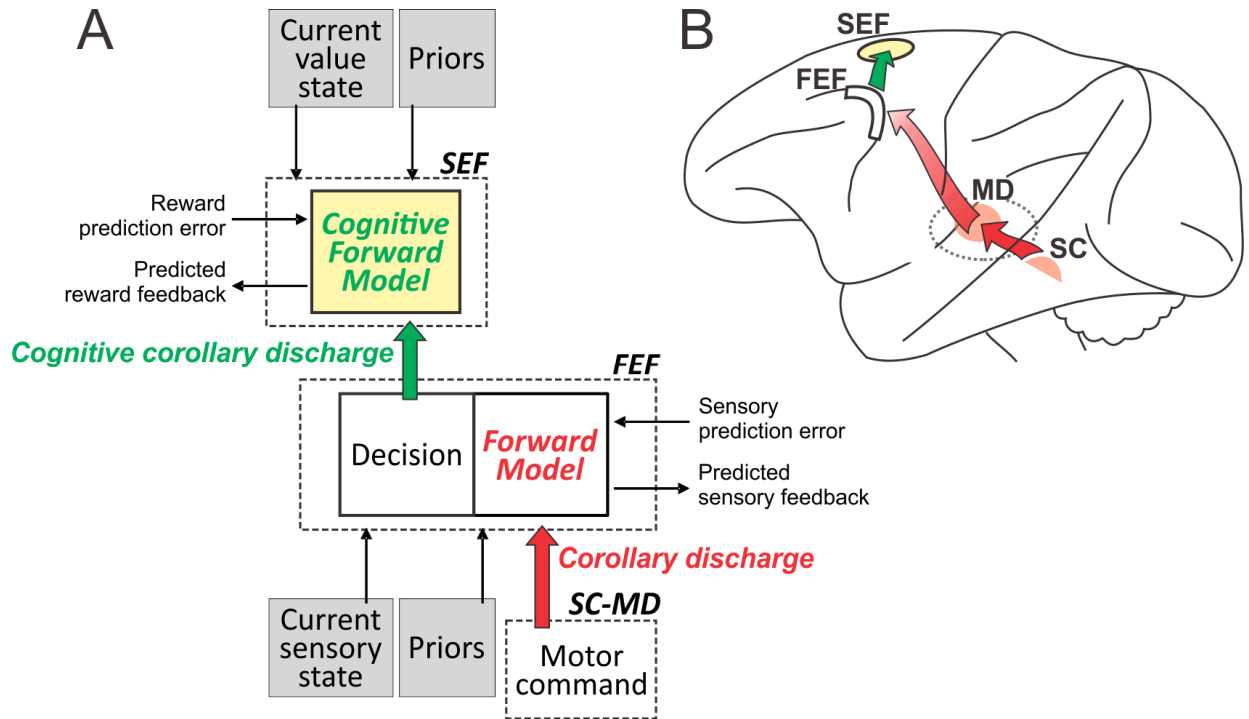
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368   **Figure 3**. FEF as a putative link between sensorimotor and cognitive forward models.

369   (A) The motor, visual, and prior signals received by the FEF would not only inform its

370   function as a visuosaccadic forward model, but also would contribute to decision-

371   making processes. Corollary discharge of decision signals in FEF could enable a

372   cognitive forward model in the SEF. (B) Neural circuit layout of this speculative cascade

373   of forward models.

374

375   Our focus has been on brain areas associated with corollary discharge pathways

376   and forward models, but that circuitry could not function as part of a cohesive internal

377   model without several other important pathways and nodes (**Figures 1** and **2**). Although

378   enumerating all of them here would be beyond the scope of this review, many brain

379   areas and circuits have properties appropriate for the other components. The

380   orbitofrontal cortex, just as one example, encodes stimulus value (73, 77, 104, 105) and

381   interconnects with the dlPFC, FEF, and SEF (reviewed by 106). This makes it a

382   compelling candidate for implementing a cognitive inverse model that compares the

383   current and desired value state to generate a decision command, a copy of which

384   becomes corollary discharge for the cognitive forward model (**Figure 2**).

385

386   **Conclusion**

387   The lessons learned from studying the SC-MD-FEF pathway have helped to define

388   exactly what corollary discharge is, why it is important, and how it may contribute to

389   broader networks. Going beyond sensorimotor systems, the same principles and a host

390   of physiological evidence support the plausibility of pathways for corollary discharge of

391   decisions. The two forms of corollary discharge have a common purpose, to guide

392   forward models, but yield different outcomes: the predicted influence of actions on

393   sensation or of decisions on reward. Identification of brain areas and pathways that map

394   onto the nodes and links of internal models could help to clarify the processes of

395   cognition in the same way that it has advanced our understanding of sensorimotor

396   behavior.

397

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