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Review

Corollary Discharge for Action and Cognition

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ABSTRACT

In motor systems, a copy of the movement command known as corollary discharge is broadcast to other regions of the brain to warn them of the impending movement. The premise of this review is that the concept of corollary discharge may generalize in revealing ways to the brain's cognitive systems. An oculomotor pathway from the brain stem to frontal cortex provides a well-established example of how corollary discharge is instantiated for sensorimotor processing. Building on causal evidence from inactivation of the pathway, we motivate forward models as a tool for understanding the contributions of corollary discharge to perception and movement. Finally, we extend the definition of corollary discharge to account for signals that may be used for cognitive forward models of decision making. This framework may provide new insights into signals and circuits that contribute to sequential decision processes, the breakdown of which may account for some symptoms of psychiatric disorders.

Keywords: Decision making, Eye movements, Forward models, Neurons, Schizophrenia, Vision

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It has been proposed that higher-level cognition in primates evolved in concert with goal-directed motor control (1) and rich representations of body state (2). Cognitive and motor systems rely on sensory information for learning about the structure of the world, and there is extensive evidence for shared substrates among sensory, cognitive, and motor processing down to the single neuron level (3–6). During behavior, sensory-to-motor signals help to specify the brain's movement commands, but at the same time reciprocal motor-to-sensory signals known as corollary discharge relay copies of the movement command to sensory areas (7). These signals keep perceptual systems informed of upcoming movement plans. Given the tight linkage between sensory-motor and cognitive operations, we propose that the strategy of one system updating another for the purpose of coordination across processing stages may be a general principle. Here we will discuss the evidence for motor corollary discharge circuits in the primate brain, their function, and the extent to which cognitive corollary discharge circuits may play analogous roles.

Why do we need corollary discharge? Animals need to perceive the world while interacting with it, but their actions change their environment. When a monkey swings through a tree, for example, the foliage rustles around her. Some of that sensory input is innocuous and the result of her actions, but some may represent a threat, such as a predator. Disambiguation of self-generated sensory signals from environmental signals is therefore fundamental to survival. Moreover, much of behavior consists of action sequences made in dynamic, uncertain environments. Waiting for information about where our effectors are at the end of each movement to plan the next one limits the speed of graceful and accurate behavior. Predictive estimation of effector dynamics, informed by corollary discharge, frees the brain from waiting for sensory confirmation of each step in a sequence.

One way to generalize how corollary discharge aids sensory disambiguation and action planning is through black box representations of system dynamics known as internal models. There are 2 main types (8). Inverse models calculate the movement needed to transition between a current and desired state. Forward models use corollary discharge of movement plans, in conjunction with other information about the system, to predict the sensory consequences of the movement (9,10). The predictions can inform subsequent inverse models that calculate corrective movements or the next movement of an action sequence. The end result is that neural processing is more proactive and less reactive, allowing for more sophisticated sensory analysis and fluid action.

In primates, eye movements are a useful, reduced model system for the study of corollary discharge. Saccadic eye movements displace the visual image on the retina, necessitating predictive mechanisms for distinguishing saccade-induced visual movement from true visual object movement. Such mechanisms could include forward models (11,12). Saccades are also made in rapid sequences and thus benefit from real-time monitoring of motor commands. For both of these purposes—perceptual and motor—a single pathway from brain stem to frontal cortex has been shown to provide corollary discharge of saccades (12–15). In this review, we use our understanding of this pathway to discuss how corollary discharge operates in the primate brain. Based on what we have learned from the visuosaccadic system, we propose a definition of corollary discharge that extends beyond action to include the monitoring of cognitive operations. Mechanisms of corollary discharge and forward models thus may provide

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

SACCADIC COROLLARY DISCHARGE

Evidence for a pathway that could transmit saccadic corollary discharge was found in experiments that electrically stimulated the brain stem's superior colliculus (SC) during recordings of neurons in the frontal eye field (FEF) of rhesus macaques. Many of the FEF neurons responded as if driven via synapses from the SC (16), which is consistent with anatomical evidence for a pathway relayed by neurons at the lateral edge of mediodorsal (MD) thalamus (17). Recordings at each step of the SC-MD-FEF pathway confirmed that it conveys temporal and spatial information about imminent saccades (14,18), and inactivation of the pathway caused deficits in saccadic corollary discharge that affected both visual processing and motor sequencing (12,15,19). The pathway therefore has all the characteristics expected from a corollary discharge circuit.

Although the focus of this review is on neural data from macaques, all of the brain areas and pathways we discuss have homologs in humans. In particular, as in macaques, the lateral edge of human MD thalamus contributes to saccadic corollary discharge as shown by lesion studies (20–23) and connects to human FEF in dorsomedial precentral sulcus of Brodmann area 6 (24) as shown by diffusion tensor imaging (25). The source of the saccadic corollary discharge is not known in humans, but the SC—which by all measures is comparable to macaque SC (26–28)—is the most likely candidate. For more on saccadic corollary discharge in humans and its relevance to behavior and pathology, see the review by Thakkar and Rolfs (29).

Source of the Pathway: The SC

Corollary discharge in the macaque SC-MD-FEF pathway originates in the intermediate layers of the SC, where neurons generate saccadic motor commands. Electrical stimulation in this region elicits saccades at extremely short latency, because only 2 synapses intervene between it and the final motor neurons (30). The intermediate layers of the SC collect information from many areas of the cerebral cortex, some of which combine sensory and contextual information to make a deliberate saccade plan while others simply relay visual signals to trigger reflexive glances (6,31). Integration of all this information in the SC creates a signal that is more tightly linked to the impending saccade than in any individual cortical area (32,33). Corollary discharge from SC to FEF is therefore the outcome of collective processing and refinement of a multitude of cortically derived, saccade-related signals (12).

Relay Node: The MD Thalamus

Corollary discharge from the SC projects to relay neurons at the lateral edge of MD thalamus. The relay neurons, for the most part, recapitulate the signals ascending from the SC (18). The population of MD thalamus relay neurons is highly concentrated, providing a convenient target for reversible inactivation of the pathway (14,15,19). Impairment of corollary discharge can be dissociated from motor impairment using the double-step task, in which subjects make saccades to the remembered locations of 2 sequentially flashed targets in the order that they appeared. To make the second saccade correctly, one must monitor where the first saccade landed, information provided by corollary discharge. It was shown that silencing MD thalamus spares the ability to make both saccades but impairs the accuracy and precision of the second one, revealing a selective deficit of corollary discharge (14,19).

Target of the Pathway: The FEF

The ascending pathway terminates in FEF layer IV. More than 90% of the neurons receiving the input exhibit visual responses (16,18), suggesting that a major role of the corollary discharge is to influence visual processing. One such influence appears to be the presaccadic remapping of visual receptive fields. As discovered originally in parietal cortex (34) and then in FEF (35), many neurons shift their visual responsiveness just before a saccade to the part of the visual field where their receptive field will land after the saccade (the "future field"). Because this presaccadic remapping links visual processing before and after a saccade, it is thought to contribute to the perception of visual continuity across saccades (36–38). Corollary discharge in the SC-MD-FEF pathway has the spatiotemporal properties needed to induce presaccadic remapping (39), and reversible inactivation of the pathway reduced FEF remapping by approximately 50% (15). In a later study, Cavanaugh *et al.* (13) found that inactivation of lateral MD thalamus also disrupts a monkey's perception of visual stability. Rao *et al.* (40) trained a recurrent neural network model to produce accurate arm movements to a visual stimulus despite intervening saccades, as an assay for visual stability. They found that the emergence of visual stability was tightly linked to that of presaccadic remapping, which itself depended on an intact pathway for corollary discharge. Together, these results support the hypothesis that presaccadic remapping contributes to visual stability and provide evidence of how disturbances to corollary discharge disrupt that stability.

OCULOMOTOR FORWARD MODEL: EVIDENCE AND OPEN QUESTIONS

The role of the corollary discharge signal provided by the SC-MD-FEF pathway can be formalized by placing it in the context of an oculomotor forward model (Figure 1A, B) (11,12). Justification for this depends on evidence consistent with 3 major features of any forward model. First, the corollary discharge would need to generate sensory predictions about the consequence of movement. This capability is demonstrated, as discussed above, by the role of the SC-MD-FEF pathway in presaccadic remapping. Neurons that remap sample, before each saccade, the part of visual space that they will "see" after the saccade (12). Presaccadic remapping in the FEF therefore provides a signal in visual coordinates that is appropriate for predicting the consequence of each saccade (11). Analysis of microcircuitry in the FEF suggests that it could generate the remapping signal locally (41), and projections from the FEF could relay the signals back to extrastriate cortex (42,43) for prediction of incoming visual input. Even though the FEF is the only known target of a corollary discharge pathway in the saccadic system, remapping is found in earlier visual areas as well. It is prevalent in the lateral intraparietal cortex (LIP) (34), visual area V4 (44,45), and medial superior temporal cortex

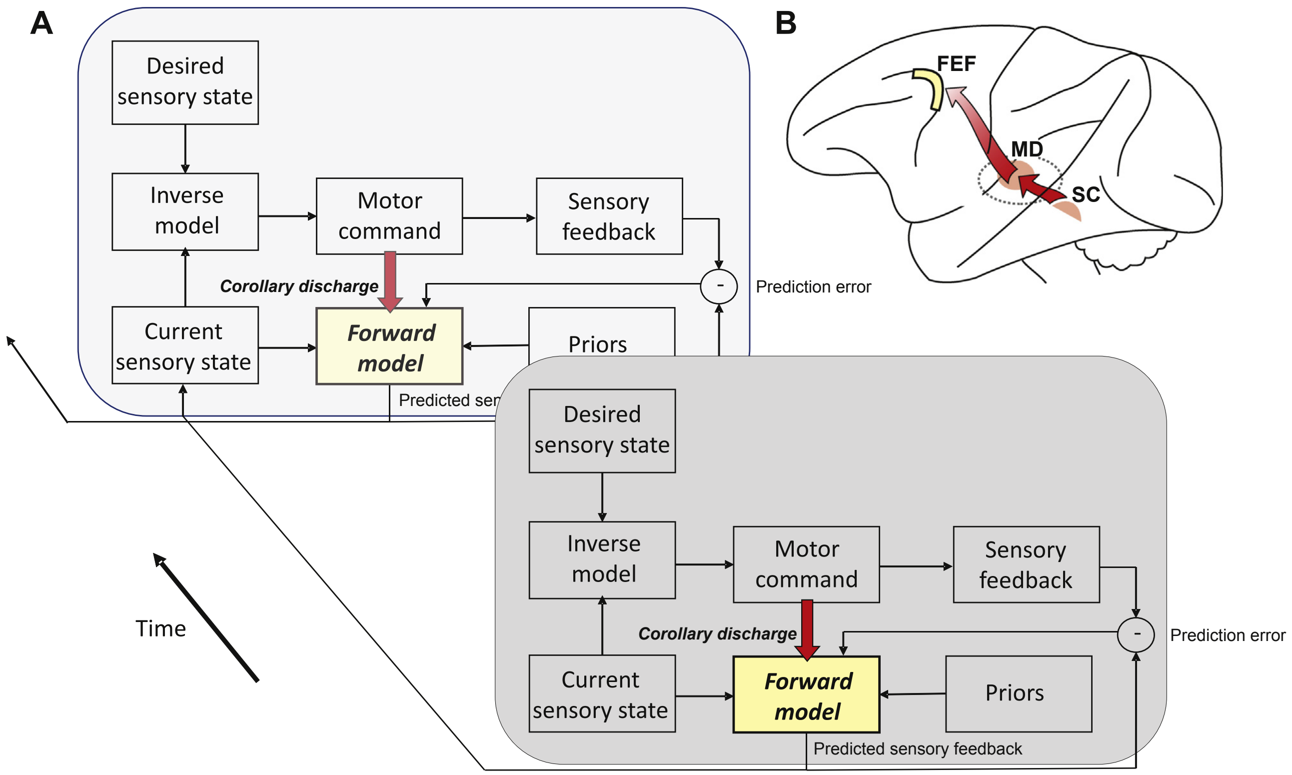

Figure 1. Sensorimotor internal models. **(A)** Inverse models generate motor commands to transition from a current sensory state to a desired sensory state. Forward models use corollary discharge, in conjunction with priors and the current sensory state, to predict the sensory consequence of an action.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

(46), but diminishes lower in the visual hierarchy from visual areas V3 to V2 and V1 [(47), reviewed in (36)]. This waning of remapping from higher to lower visual areas is consistent with its possible function as a top-down mechanism for prediction of visual input. Presaccadic remapping has been reported in human visual cortex as well (48,49), with a similar decrease in remapping from higher to lower visual areas (49).

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 eye 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 environment could include knowledge about objects in the world, such as their propensity to move. Animals often move, for example, while rocks rarely do. Accounting for the intrinsic nature of objects would improve predictions about their states across saccades. Rao *et al.* (50) tested whether human subjects use priors in this way by having them make a saccade to a visual target and report whether the target's location (spatial state) changed during the saccade. Targets had varying probabilities of moving, from 0.1 to 0.9, that were matched to their color. When the subjects were informed of the color-probability assignments, thus instilling priors about object movement, their sensitivity at detecting the state change became a function of the priors (50). This indicates that the oculomotor forward model incorporates priors about the state of the environment, even to the level of individual objects, when predicting the sensory consequences of saccades.

A final component of any forward model is that the predicted sensory consequence of a movement is compared with the actual sensory consequence—the "reafferent" response. The difference between these signals, the prediction error, is used to update future predictions. Crapse and Sommer (51) tested whether FEF neurons make such comparisons about predicted versus reafferent visual responses across saccades. They recorded from FEF visual neurons in monkeys that made saccades to visual targets in the presence of a behaviorally irrelevant visual probe. During each saccade, the probe would stay still or move, but after the saccade, it was always at the center of the neuron's postsaccadic receptive field. Because the postsaccadic location of the probe was constant, the null hypothesis was that reafferent responses would be constant. The result, however, was that reafferent responses varied as a function of how much the probe moved during the saccade. The reafferent responses also were sensitive to other changes in the probe (size or color) across saccades. Hence, FEF neurons exhibit a robust prediction error signal about transsaccadic changes of visual stimuli.

Multiple lines of evidence therefore support the hypothesis that corollary discharge in the SC-MD-FEF pathway contributes to an oculomotor forward model. More studies are needed to test this hypothesis, integrate the individual lines of evidence, and identify specific circuits and mechanisms of the forward model.

One way to test the oculomotor forward model hypothesis would be to check whether presaccadic remapping is needed for computing the prediction error signaled by FEF neurons. Is that error signal computed through a comparison of future field responses and postsaccadic receptive field responses? This could be tested by inactivating MD thalamus to reduce remapping in FEF (15) while examining the prediction errors reported by FEF neurons (51). If the computation of prediction error signals requires presaccadic remapping, it should be reduced by MD thalamus inactivation. Many other mechanistic questions need to be studied, as well:

1. How are priors about the environment included in the feedback prediction? Where are these priors represented and how do they combine with the spatial prediction generated by anticipatory remapping?
2. How and where is the prediction error signal computed? A prediction error is the difference between the feedback prediction and the incoming input. Thus, a prediction error might be generated at any stage in the visual hierarchy.
3. How does the prediction error signal update future predictions? A prediction error across a saccade could arise because of an incorrect corollary discharge signal or because of incorrect information about the state of the system. Solving this credit-assignment problem would require knowing the relative accuracies of each of these signals and updating them accordingly. Alternatively, it is possible that the incoming sensory signal itself is unreliable, which should make the prediction error less likely to update one of the predictive signals. Bayesian models formalize this prediction. Within a Bayesian model, the prior is equivalent to the prediction; the likelihood, to the incoming signal; and the posterior, to the prediction error (52). Bayesian models also predict that perception is closest to the posterior. A simulation study by Niemeier *et al.* (53) showed that saccadic suppression is a consequence of accounting for the reliability of eye movements, thus providing evidence for the implementation of a Bayesian model in the oculomotor system. Whether a prior about the environment and the incoming input are combined in a Bayesian manner, however, remains unknown.

Learning more about oculomotor forward models also could improve our understanding of the circuit basis of psychiatric disorders. Eye movements are abnormal in schizophrenia (29,54), and several of the disorder's symptoms are thought to result from impairments of corollary discharge and forward models [for reviews, see (55–58)]. In anticipation of the broader use of these concepts for explaining psychiatric conditions, it seems timely to revisit the definition of corollary discharge and assess its applicability to signals within cognitive networks of the brain.

COGNITIVE FORWARD MODEL: PROPOSAL AND IMPLICATIONS

Although corollary discharge originally referred only to copies of motor commands (59), that strict conception seems outdated. Even within the saccadic system, corollary discharge from the SC originates at least 2 synapses upstream from the extraocular muscles and consists of a mixture of visual responses, delay activity, and movement signals (18), suggesting that corollary discharge as it exists neurally is more nuanced than was imagined theoretically. We propose that corollary discharge, broadly speaking, is any copy of a neural signal that is conveyed for informational purposes and state updates.

Consider two successive tasks, task A and task B, where performance of task B is contingent on task A. A "task" may be any distinct operation performed by the nervous system, from tapping a finger to deciding where to eat lunch. Corollary discharge of task A would be a neural signal that meets the following criteria: 1) It must be a copy of the command that produces task A, in that it carries the same information as the command itself. 2) Execution of task A must not depend on the signal. 3) Execution of task B must depend on the signal. 4) The signal must be produced regardless of whether task B follows task A. The first 2 criteria require that corollary discharge reflects the performance of task A without causing it. The third criterion requires that the corollary discharge signal be useful, in that it is needed for some task B. The fourth criterion limits corollary discharge to signals that are produced whenever task A occurs rather than only in anticipation of a specific task B, to exclude specialized, trained signals that link the tasks. In the case of saccadic corollary discharge, for example, task A is the generation of a saccade. The SC can be said to produce a corollary discharge of the task because its ascending signals are 1) copies of the saccade vector, 2) irrelevant to moving the eyes, 3) necessary for generating a second saccade in the double-step task and remapping of visual receptive fields, and 4) obligatory.

Applied to neural systems that accomplish the task of decision making, the framework could help to identify cognitive corollary discharge signals. The plausibility of such signals is suggested by a range of studies, across species, showing that when individuals make decisions, they self-monitor them (60–65). The neural signals that monitor decisions do not drive those decisions (66–69) but seem to provide a more informational function that helps to guide subsequent decisions (70,71). Such performance-monitoring signals have the potential for meeting the criteria of a corollary discharge signal in the cognitive domain.

In the saccadic system, corollary discharge signals inform visual processing and guide the planning of subsequent saccades through putative forward models. Analogously, when we say that corollary discharge of a decision may guide subsequent decisions or other tasks, it implies an intermediary mechanism, which could be a cognitive forward model. What would such a model look like? One well-studied type of decision is made to transition from the current value state to a desired higher value state. This value transition may take the form of gaining reward or avoiding punishment. In this context,

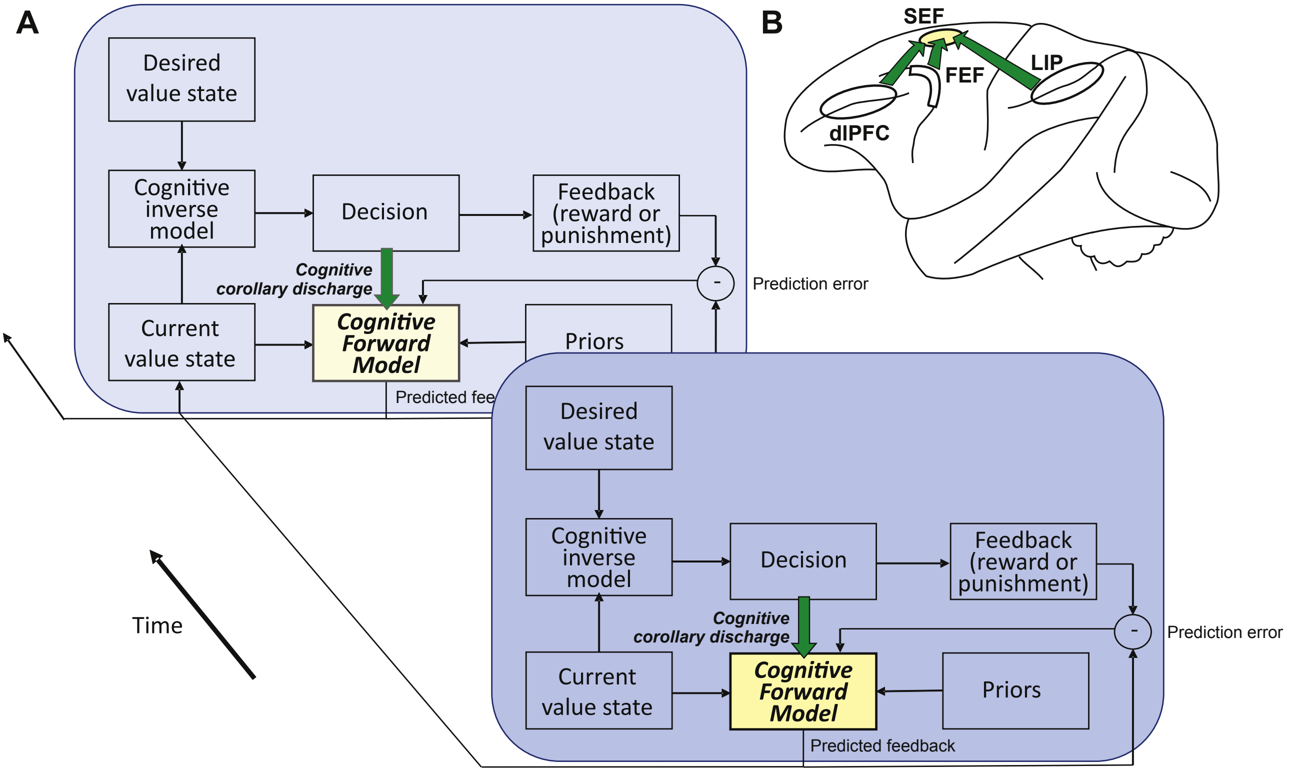

Figure 2. Cognitive internal models. **(A)** An example of a cognitive forward model that would use cognitive corollary discharge of decisions to predict their value consequences. **(B)** One candidate area for contributing to this type of cognitive forward model is the supplementary eye field (SEF). Corollary discharge of decisions could arrive from multiple possible areas including the dorsolateral prefrontal cortex (dlPFC), the frontal eye field (FEF), or lateral intraparietal cortex (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 area 6 (24,72), dlPFC in the middle frontal gyrus portion of Brodmann areas 9 and 46 (73,74), FEF in dorsomedial precentral sulcus within Brodmann area 6 (24), and LIP in Brodmann area 7 (75).

a cognitive forward model would generate predictions of the value consequence of a decision, using a copy of the decision command (Figure 2A) (72–75).

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 coordinates. The model would yield a predicted value state that could be used as the current value state even before reward is received, allowing decisions to be planned in quick and accurate sequences. The difference between the predicted value and the reinforcement that is eventually received, the prediction error, would be relayed back up to local decision centers to update subsequent decisions and predictions. There is widespread evidence for the existence of reward prediction and reward prediction error signals across various brain areas (76–81). Indeed, reward prediction error is thought to be a key driver of learning, that is, the updating of subsequent predictions to match the outcome. Although there are influential computational models of how reward prediction error signals might be generated (82) and some recent efforts toward investigating this in neural circuits (83), we do not have a clear understanding of the components that go into the calculation of reward prediction error in the brain. A cognitive forward model that generates predictions about decision outcome, and in turn, prediction errors, provides a plausible explanation. Cognitive forward models can be extended to include decisions across sensory modalities or more abstract decisions to transition between thought states. Dysfunction of these models might then explain the aberrant internal states observed in many complex psychiatric disorders.

For decisions involving vision and eye movements, the supplementary eye field (SEF) is a possible locus for the implementation of a cognitive forward model (Figure 2B). Simulation and inactivation studies suggest that it is not centrally involved in eye movement generation [reviewed by (72)], yet during visuosaccadic tasks its neurons carry signals that correspond to decision monitoring, reward prediction, received reward, and reward prediction errors (68,69,79,84,85). A recent study also linked the activity of neurons in the SEF to the generation of error-related negativity, an electroencephalography-based measure of prediction errors (86). Abnormal error-related negativities in patients with schizophrenia are thought to reflect deficiencies in the self-monitoring of thoughts and actions (87–90) and might arise from dysfunction of a cognitive forward model. Such a forward model, however, cannot function without input from cognitive corollary discharge, just as visual receptive fields cannot remap presaccadically without information about the upcoming saccade.

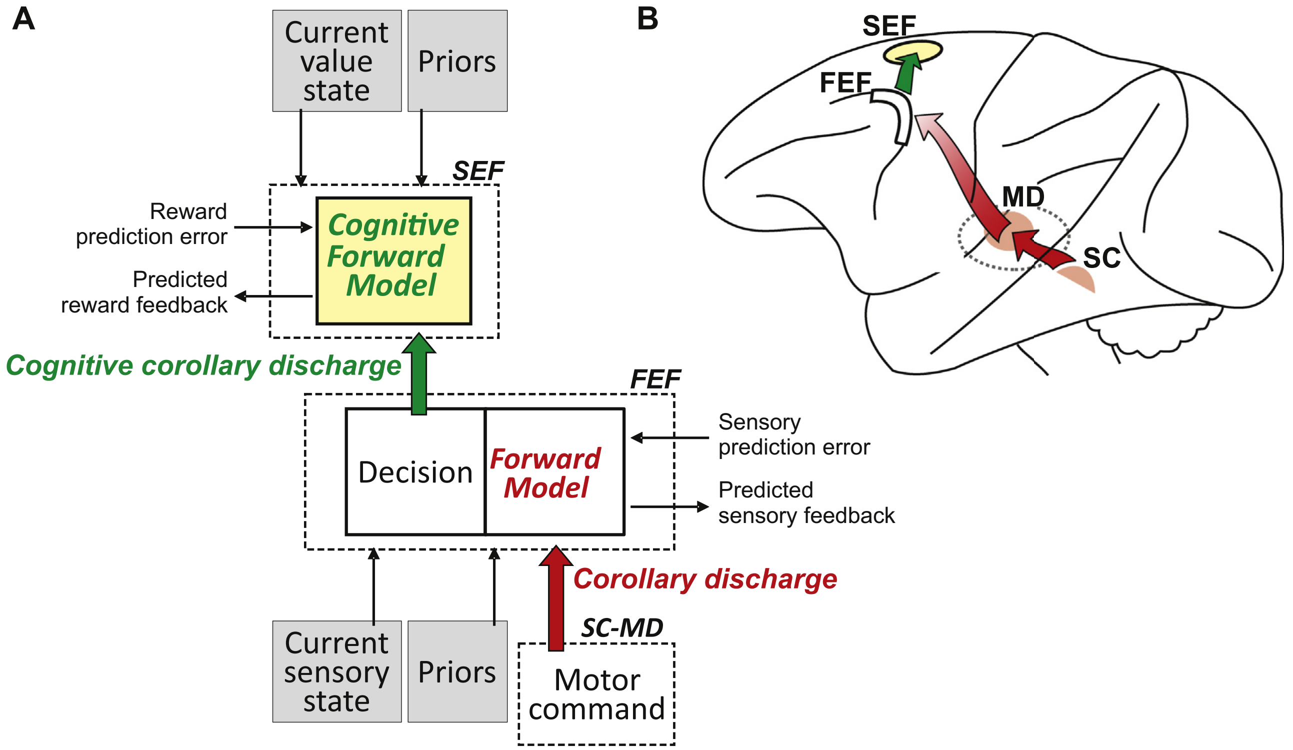

Figure 3. Frontal eye field (FEF) as a putative link between sensorimotor and cognitive forward models. **(A)** The motor, visual, and prior signals received by the FEF would not only inform its function as a visuosaccadic forward model, but also contribute to decision-making processes. Corollary discharge of decision signals in FEF could enable a cognitive forward model in the supplementary eye field (SEF). **(B)** Neural circuit layout of this speculative cascade of forward models. MD, mediodorsal thalamus; SC, superior colliculus.

Corollary discharge of decisions could arrive from several candidate areas including dorsolateral prefrontal cortex and LIP (91,92), but a particularly interesting source would be the FEF. In addition to its sensorimotor integration functions, the FEF appears to contribute to sensorimotor decisions (93–96). The information that the FEF receives about upcoming saccades, the visual scene, and priors would be useful for both its own forward model operation and its decision-making functions. Corollary discharge of the latter could inform the SEF cognitive forward model (Figure 3A) (97), meaning that the FEF would serve as the terminus of one forward model and the origin of corollary discharge for another (Figure 3B). This cognitive corollary discharge might be relayed by a direct connection between the 2 regions (98) or indirectly via a transthalamic pathway [(99,100), reviewed in (58)]. In support of the latter, monkeys with lesions to MD thalamus are impaired in exploiting information about their recent decisions in an adaptive decision-making task (101). Other nodes in the oculomotor system, such as LIP, could provide similar interfaces between sensorimotor and cognitive forward models. Neurons in LIP remap their visual receptive fields (34) and carry signals about both decisions (102,103) and monitoring of decisions (67). However, for LIP to function as a sensorimotor forward model, it would have to receive saccadic corollary discharge, but no such pathway to LIP has been discovered yet. Regardless, the shared neural substrate of FEF (and possibly LIP and other areas), via their joint roles in forward models, might provide a direct mechanism by which cognitive processing builds on sensorimotor integration.

Our focus has been on brain areas associated with corollary discharge pathways and forward models, but that circuitry could not function as part of a cohesive internal model without several other important pathways and nodes (Figures 1 and 2). Although enumerating all of them here would be beyond the scope of this review, many brain areas and circuits have properties appropriate for the other components. The orbitofrontal cortex, just as one example, encodes stimulus value (73,77,104,105) and interconnects with the dorsolateral prefrontal cortex, FEF, and SEF [reviewed by (106)]. This makes it a compelling candidate for implementing a cognitive inverse model that compares the current and desired value state to generate a decision command, a copy of which becomes corollary discharge for the cognitive forward model (Figure 2).

CONCLUSIONS

The lessons learned from studying the SC-MD-FEF pathway have helped to define exactly what corollary discharge is, why it is important, and how it may contribute to broader networks. Going beyond sensorimotor systems, the same principles and a host of physiological evidence support the plausibility of pathways for corollary discharge of decisions. The 2 forms of corollary discharge have a common purpose, to guide forward models, but yield different outcomes: the predicted influence of actions on sensation or of decisions on reward.

Identification of brain areas and pathways that map onto the nodes and links of internal models could help to clarify the processes of cognition in the same way that it has advanced our understanding of sensorimotor behavior.

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ARTICLE INFORMATION

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