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Corollary discharge circuits in the primate brain

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Movements are necessary to engage the world, but every movement results in sensorimotor ambiguity. Self-movements cause changes to sensory inflow as well as changes in the positions of objects relative to motor effectors (eyes and limbs). Hence the brain needs to monitor self-movements, and one way this is accomplished is by routing copies of movement commands to appropriate structures. These signals, known as corollary discharge (CD), enable compensation for sensory consequences of movement and preemptive updating of spatial representations. Such operations occur with a speed and accuracy that implies a reliance on prediction. Here we review recent CD studies and find that they arrive at a shared conclusion: CD contributes to prediction for the sake of sensorimotor harmony.

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Introduction

Imagine a monkey leaping through the forest canopy. As it moves, branches brush against its skin, leaves rustle at its hands and feet, and patterns of light and shade alternate across its eyes (Figure 1a). In principle, the monkey should be startled by these sensory events. The activation of its skin receptors could be interpreted as due to an insect landing on its leg and the sounds and shadows as due to a predator looming. Surprisingly, the monkey does not find these sensory events alarming; they are expected, partly because the monkey has access to an internal report of its own movements called corollary discharge (CD).

Each of the monkey's movements is initiated by motor commands that travel from movement areas of the brain out to the periphery to contract the appropriate muscles. Neural copies of the movement commands – the CD

signals – are issued simultaneously and travel in the opposite direction, impinging upon sensory brain areas (Figure 1b). The CD information tells the sensory areas about the upcoming movements and allows them to prepare for the sensory consequences of the movement. As a result, our monkey in the forest is not surprised by the brush of the branch, the rustle of the leaves, or the change in shade. Were the monkey at rest or moving passively – for example, sitting on a branch that sways in the breeze – the same sensory events would be startling indeed.

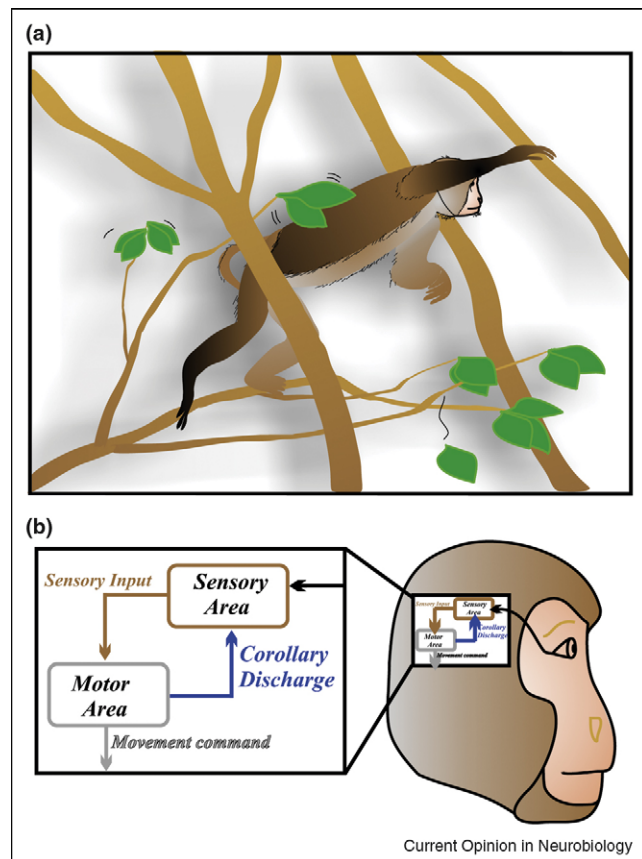
As a theoretical concept, CD has a rich history [1]. Behavioral and psychophysical evidence for CD has accumulated over a century and received a significant boon in 1950 when two teams of researchers working independently and on different continents arrived at the same conclusion: Motor and sensory systems require reciprocal coordination, implying that motor signals travel to sensory structures [2,3]. Now, decades later, we know the motor-to-sensory signal to be quite ubiquitous as demonstrated by a wealth of direct physiological evidence collected from a menagerie of species [4–6]. In this review we examine recent behavioral and physiological studies of CD in primates and place an emphasis on its role in prediction. We close by considering computational treatments of the concept.

CD and human behavior

Human psychophysical studies have provided much insight into CD function and its roles in two operations: resolving ambiguity in the origin of sensory inputs and enabling proper motor performance. Many of these studies have focused on the visuomotor networks of primates, particularly on those that mediate smooth pursuit and saccadic eye movements. Eye movements are beneficial in permitting detailed analysis of objects by the fovea, but they are costly, too, as they generate retinal image motion that is indistinguishable from real object motion. We do not, however, experience the startling percept of world motion as our eyes rotate; instead we enjoy a percept of stability. This implies a corrective mechanism within the oculomotor networks of the brain. One model of this mechanism, based closely on the classical concepts of Efferenzkopie ('efference copy') by von Holst and Mittelstaedt [3] and Willensanstrengung ('effort of will') by von Helmholtz [7], postulates a cancellation process mediated at least partly by an internal reference signal [8]. This internal reference signal, generated from a CD that represents each eye movement, is a prediction of the imminent retinal image motion. The prediction is compared to the actual retinal motion; if the two signals cancel, then no net motion of the visual world is perceived. If they

2 Motor systems

Figure 1



Action and perception. **(a)** A monkey in the forest has obvious need for sensorimotor coordination. Every movement results in an inundation of sensory inputs that must be discriminated and referenced so that the monkey can proceed with the next. **(b)** Corollary discharge provides a means for this coordination by apprising sensory areas of the goings-on of movement areas. Just as a movement command is issued, a copy of that movement command (corollary discharge) is routed in the opposite direction to inform the appropriate sensory area. This sort of signalling closes the sensorimotor loop and makes sensorimotor operation possible.

do not cancel, then the residual is experienced as motion of the world. Psychophysically, evidence for the internal reference signal has been provided in the smooth pursuit system where it has been shown to be rather plastic [9]: the gain of the CD can be manipulated quite readily in the laboratory. As predicted, when the gain is adjusted, false eye movement-induced perceptions of world motion are experienced [9]. This ability to manipulate the internal reference signal has been exploited by investigators to pinpoint the anatomical sites of retinal signal/internal reference signal comparison and cancellation. Evidence suggests that it resides in late parts of the cortical hierarchy such as medial superior temporal area (MST) and parieto-insular-vestibular cortex [10–12].

An adaptable reference signal also serves a purpose on the motor side of things. Movements are often too fast to be

under strict control by external feedback from sensory receptors. They require internal feedback of motor commands, which CD provides. As a ballistic sort of motor expression, the saccadic eye movement is a case in point. Theoretical treatments have long postulated a motoric internal reference signal, representing the effector's (i.e. the eye's) instantaneous position, that is utilized by the brain to monitor the trajectory of the movement [13,14]. This sort of monitoring is posited to consist of a forward model of the oculomotor system that uses CDs of the saccade to generate predictions of the expected sensory outcome. The predictions are then used to update the saccade, by implementing corrections mid-flight. A prediction of this hypothesis is that the forward model should adapt when its predictions systematically fail, that is, when they do not match the expected sensory feedback. Shadmehr and co-workers tested this hypothesis in a task that artificially introduces discrepancies between the predicted and actual sensory outcome, the saccadic adaptation task [15^{*}]. Forward model involvement would be betrayed by saccades with systematic curvatures revealing mid-flight correction to the target's new position. They found that saccadic adaptation was preceded by forward model adaptation, a result manifested in saccades with characteristic curvature. Similar adaptations occur for visually guided limb movements [16,17].

CD also plays a part in coordinating the skeletomotor and somatosensory systems. A prominent role is in permitting the primate to distinguish between tactile inputs that are due to self from those due to something else. A psychophysical correlate of this interaction is elevated thresholds to somatic stimulation during active movement, a type of sensorimotor attenuation [18]. A pair of causal studies in humans, one using transcranial magnetic stimulation (TMS) to delay movement execution [19^{*}] and another using ischemic nerve block to silence proprioception [20^{*}], revealed that modulation is mediated by premotor cortical inputs to somatosensory cortex. These inputs modulate somatosensory neurons often by suppression and may consist of predictions of the sensory consequences of the movement [21,22].

Vocalization and auditory systems must also coordinate their activities. CD mechanisms involving speech production and auditory regions, play such a coordinative role in distinguishing auditory experiences resulting from self-generated vocalizations from those arising from other-generated speech sounds. Evidence for this interaction is provided by neurons in auditory areas that are suppressed during self-generated vocalizations, yet remain fully response for comparable stimulation produced by conspecifics [23,24]. This observation extends to language areas of the human brain [25] that exhibit a dampening of the so-called N100 component of the auditory event related potential during self-vocalization [26]. Interestingly, this dampening is significantly reduced in schizophrenic

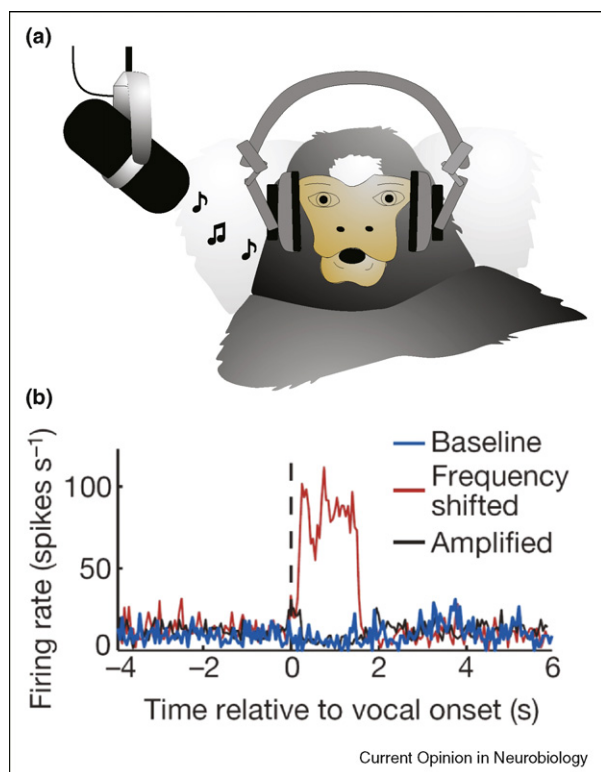
patients suffering from auditory hallucinations, betraying a reduction in speech production/auditory coordination [27,28^{*}]. An alteration in this coordination may result in internally generated events such as thoughts being experienced as having an external source. This may serve as a basis for certain aspects of the disease pathology such as auditory hallucinations and self-monitoring deficits.

CD and mechanism

In order to better address mechanism, many researchers have turned to another primate species: the monkey. Studies in the auditory cortex of the marmoset, for example, have provided insights into the neural correlates of auditory–vocal interactions (Figure 2a). As mentioned, neurons throughout the auditory cortex are inhibited during self-generated vocalizations, a possible neural correlate of self-monitoring [23,24]. Recent work has provided more insight into this process and shown the

suppression to be part of a mechanism that actually increases the sensitivity of these neurons to auditory feedback, specifically to deviations from the *predicted* feedback [29^{**}]. As the marmoset vocalizes, the frequency tuning of the neurons transiently shifts and seems to monitor for deviations from the expected auditory feedback. When the actual feedback matches the expected feedback, the neurons are silent, that is, suppressed (Figure 2b, blue trace). But when the feedback differs, as revealed through artificial manipulation, the neurons fire, signalling the disparity (Figure 2b, red trace). This sort of disparity detection suggests that the neurons are reporting prediction error or deviations from the expected outcome. Similar processes are at work in the primate visuosaccadic system in which CD signals induce a transient change in visual-related activity during saccades to better predict the postsaccadic visual scene, that is, expected visual feedback (more below).

Figure 2



Shifting RFs and the auditory system (a) 'Marmoset in a recording studio.' Investigators recorded from auditory cortical neurons as a marmoset vocalized. The auditory feedback from the vocalization was relayed to the marmoset without delay under both normal and altered conditions. (b) Peristimulus time histogram exhibiting the basic effect. This auditory cortical neuron was suppressed during normal vocalization (blue trace). However, when the auditory feedback of the vocalization was shifted in the frequency domain, the neuron exhibited a large increase in firing rate (red trace). The neuron's frequency tuning was transiently altered at the outset of the vocalization by a CD, rendering it sensitive to deviations from the expected auditory feedback, an example of a shifting RF in the auditory frequency domain. Adapted from ref. [29^{**}].

As mentioned, saccades are a second common visuomotor behavior of the primate, and like the smooth pursuit system, they require the discriminative powers of CD. CD signals have a hypothesized role in distinguishing visual scene displacements due to the saccade from those due to real object motion in the world [30,31^{*}]. At the outset of each saccade, advance warning is provided by CD, mediating a compensatory procedure to cancel the percept of visual-scene displacement. Crucial components of this procedure are thought to be neurons of the visual system that transiently shift their receptive field (RF) before each saccade. Although a typical RF is firmly retinotopic and samples a new part of the visual field only after the eye moves, shifting RFs are dynamic and start sampling the new RF location even before a saccade. By sampling the same region of space both before and after the saccade, shifting RFs are thought to perform a comparative operation that leads ultimately to a stable visual percept. Such neurons are found throughout extrastriate and frontal cortex [30,32,33] and, because the RF shifts before the saccade and in a direction and amplitude that matches the imminent saccade, the shift must require CD. At least some of this CD is provided by a midbrain-derived pathway impinging upon the frontal eye field (FEF), an area involved in visual processing and eye-movement control [31^{*},34]. It has been postulated that inactivation of this pathway would result in the disorienting percept of visual scene displacement with each saccade [31^{*}]. Under this condition, monkeys trained to detect object motion during saccades should report that stationary visual stimuli move with each saccade. This would be a direct test of the CD/shifting RF visual-stability hypothesis.

Saccadic sequences also require the use of internal feedback signalling mediated by CD. The relative positions of objects must be updated after each intervening saccade, so the primate must continuously update its internal

4 Motor systems

record of the current saccade in order to facilitate planning of the next. Retinal information is too slow to be of any use, and ocular proprioception does not seem to be involved (reviewed in ref. [35]), so the system requires CD of each saccade to properly update the spatial representation. In the laboratory this sort of phenomenon has been studied with the double-step task in which the subject is required to saccade by memory to the locations of two previously flashed sequential targets [36]. This particular task requires a retracing of the flash sequence without the aid of *sensory feedback*, but rather with the only feedback available: *internal feedback* provided by CD. Inactivation and lesion studies indicate that some of these CD signals are provided to the FEF from the same midbrain-derived pathway used for shifting RFs [37–40]. When the pathway is compromised by transiently inactivating its relay node in MD thalamus, the second saccades are altered, exhibiting patterns of rotational deviation consistent with deficits in taking the previous saccade into account. Other thalamic nuclei, such as VL nucleus and area X, may convey subcortically derived CD too, but these seem to differ from MD in being more involved in the timing of self-initiated saccades rather than updating the spatial representation [41].

Further support for CD involvement in visuospatial performance is provided by stimulation studies in the FEF [42]. Subthreshold microstimulation during the delay period of memory tasks results in displacements of memory-guided saccades in a manner consistent with introduction of fictive CD signals: the monkey executes the planned saccade as if another saccade had been performed during the interim. The fact that stimulation does not disrupt the memory trace itself, suggests that the FEF may be more important as a locus of updating spatial representations and the exportation of these computational outcomes to other brain areas. In this sense, the FEF may be crucial as a gateway for exporting visuosaccadic predictions to the rest of the brain. We discuss this in more detail in the succeeding section.

CD and computation and beyond

Several computational studies have modeled CD-dependent processes and suggested how the nervous system utilizes CD for functions such as spatial updating [43], and perisaccadic perception [44]. But a question that remains is, from a computational perspective, what is CD? While practical criteria for identifying CD at the behavioral and neuronal levels have been provided [45] a fair question to pose at this juncture is whether there is a more general definition of CD. Stated differently, is there a function common to all instantiations of CD that captures the essence of what CD actually is and does?

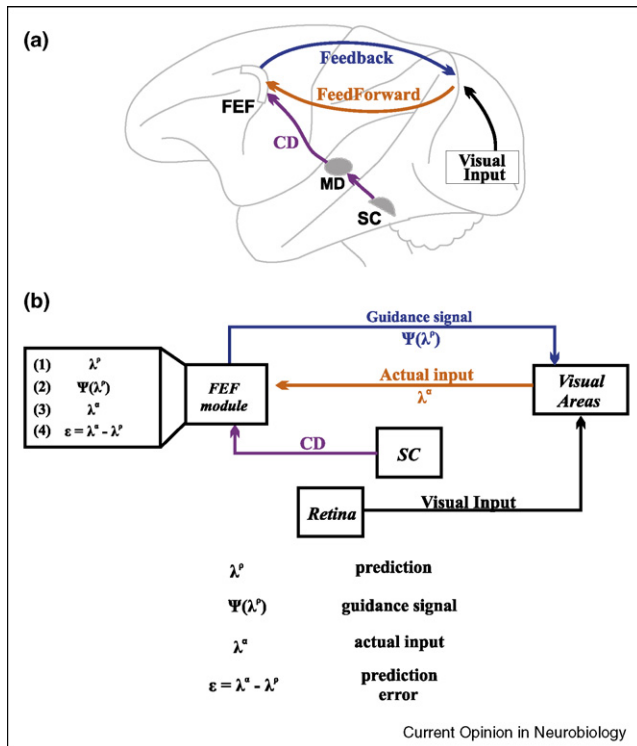
The reviewed psychophysical, physiological, and causal studies provide possible answers to this question. Some common principles are that CD is a signal involved in

motor planning, and most prominently, in distinguishing those sensory inputs that result from self from those that result from something else. This latter function is illustrated best in the shifting RFs of the auditory [29] and visual systems [30,31,32,33], the predictive reference signals of the smooth pursuit system [8], and the forward model motoric processes of the saccadic system [15]. These mechanisms necessitate a predictive component, as they must generate and compare the *expected* consequences of the movement, be it motor or sensory, with the actual consequences, and they must do so in a rapid manner despite processing delays. Deviations from the prediction ultimately manifest at both the physiological and behavioral levels as bursts of action potentials where silence would otherwise reign [29] and shifts in psychometric curves [8,15]. So a short answer is that the underlying function of all CD signals is the prediction of motor consequences. This formulation, with its reliance upon prediction and comparison, is conceptually similar to the forward model framework prevalent in current sensorimotor discussions whereby CDs of movement commands are converted into expected sensory outcomes [14].

If CD is motor-related prediction, how might these predictive operations be implemented? Computationally, they would most probably have to be inferential in nature, that is, probabilistic. Probabilistic computations, such as those based on empirical Bayesian principles, would enable rapid predictions to be generated [46,47]. These computations would allow prior and conditional probability distributions, stored in neural networks, to be utilized to generate a posterior distribution, that is, the outcome expected on the balance of known probabilities and other inputs (in other words, a prediction). Comparisons between the predicted outcome and actual outcome, so prominent in the reviewed CD circuits, could then proceed. Psychophysical and physiological evidence provides support that such computations are indeed performed by the brain under a variety of contexts [47–49].

We have proposed elsewhere that predictive operations, grounded in such probabilistic inference, are implemented in the primate visuosaccadic system for the purpose of constructing a stable transaccadic percept [50]. At the center of the model are CD and shifting RFs of the FEF, and we propose they together constitute an inferential architecture that engages in predictive coding. Theoretically, these components enable predictions of the future scene (postsaccadic scene) to be generated on the basis of predictive, probabilistic extrapolations from the current scene (presaccadic; Figure 3). These predictions provide activity constraining expectations to the rest of the brain and may contribute to a percept of stability. The model predicts that deviations (prediction errors) from the expected visual input are manifested in the postsaccadic visual responses of FEF

Figure 3



Corollary discharge and predictive computations in the visuosaccadic system. (a) Lateral view of macaque brain illustrating the interactions between the frontal eye field (FEF) and the posterior lobes. Triggered by CD, the FEF exports predictive signals to the posterior lobes via feedback connections. The posterior lobes report back to the FEF about the actual visual input via feedforward connections. (b) Corresponding schematic diagram depicting the computational roles of the FEF. FEF module inset: (1) A series of computations, triggered by CD from the midbrain and enabled by shifting RFs, results in a prediction of the postsaccadic scene (λ_p) on the basis of information extracted from the current or presaccadic scene. (2) The prediction is then convolved with a forward model (Ψ) to yield guidance signals ($\Psi(\lambda_p)$) that are imposed upon the posterior lobes. This signal constrains the state space of the posterior lobes and biases the operations performed within them. (3) Once the saccade is complete, information about the actually occurring postsaccadic scene (λ_a) is routed to the FEF. (4) The FEF compares the input representing the actual postsaccadic scene with the initial prediction ($\epsilon = \lambda_a - \lambda_p$). This is useful for calibration, error correction, and the detection of unpredicted visual events.

neurons (analogous to the auditory disparity detectors of the reviewed marmoset study [29]). Preliminary data from our laboratory provide support for such a large-scale prediction error theory of transaccadic stability [51].

Future computational studies will continue to provide further insights into CD and its role in predictive computations of the primate brain. Together with behavioral and neurophysiological studies, including those reviewed here, the modeling work should help to explain in a more formal way how CD contributes to sensorimotor harmony as primates interact with the world. The field of motor control will benefit from expanded efforts to determine

not only how sensory analysis and spatial cognition influence movements, but also how movement signals influence sensory analysis and spatial cognition.

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