Symposium

Suppressing Sensation during Action across Species and Sensory Modalities: Predictive and Nonpredictive Mechanisms of Sensory Modulation

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Perception and action are deeply intertwined processes that require the nervous system to distinguish between self-generated (reafferent) and externally generated (exafferent) sensory inputs. To maintain accurate perception during movement, the brain must attenuate predictable sensory consequences of its own actions while remaining sensitive to unexpected external events. Reafference attenuation is a temporally precise process that suppresses expected feedback, facilitating the detection of novel stimuli. This review examines reafference attenuation across species (rodents, nonhuman primates, and humans) and sensory systems (vestibular, auditory, and tactile). We also discuss sensory gating (or sensory suppression), a broader and often less selective mechanism that inhibits both self- and externally generated inputs. Although both mechanisms reduce sensory inflow during movement, they differ in function, specificity, and temporal dynamics, and despite growing insight into their underlying circuitry, important questions remain about their generality and implementation.

Introduction

Perception and action do not form a linear sequence of processes. They rather cause each other reciprocally and, thus, form predictive loops. The principal idea of a predictive loop is that the animal must internally represent the goals of its actions, predict their effects, compare them to what actually happened, and use this information to improve motor performance. For the survival of an animal, it is important for it to know whether a certain sensation was produced by its own action (sensory reafference) or whether it was due to an event in the world (sensory exafference; Fig. 1). To solve this, the brain has evolved as a nested set of feedback control loops, in effect endowing animals with some sense of agency. Evidently, these loops underlie a wide range of behaviors, such as motor control, goal-directed actions, foraging, strategic planning, and social interactions. These loops have typically been studied and characterized in isolation, and attempts to study their interaction have been comparatively rare.

The principal idea of a predictive loop was introduced early by Helmholtz' "inferential brain," Holst and Mittelstaedt's "reafference principle" (von Holst and Mittelstaedt, 1950), and Sperry's "efference copy" (Sperry, 1950). These ideas emphasized that perception is shaped not just by incoming sensory data but also by internal predictions based on motor commands. They gave rise to later theoretical elaborations, intended as an explanation of neocortical circuits, under catchphrases like "Helmholtz machine" (Dayan et al., 1995), which models perception as a form of probabilistic inference, and "Active inference" (Parr and Friston, 2019), a theory according to which the brain minimizes prediction error through both perception and action. The cerebellum, on the other hand, inspired ideas like "Feedforward models" and "Kalman filters" that emphasized fast, anticipatory responses based on internal models of the body and environment (Bays and Wolpert, 1993; Wolpert et al., 1998; Körding and Wolpert, 2004), and their combination called "State estimation" through which the brain infers the current state of the body or world from noisy and delayed sensory inputs (Shadmehr and Mussa-Ivaldi, 2012). They contributed algorithmic approaches from the field of engineering for prediction and comparison respectively. Under the name of "comparator model," feedforward models also featured in discussions about cognition, agency, and consciousness, where internal predictions are compared with sensory feedback to assess authorship of actions (Synofzik et al., 2008).

A predictive loop must minimally include two interconnected algorithmic elements: The first element holds the learned associations between actions and their sensory consequences and computes predictions, which in turn are projected onto the second
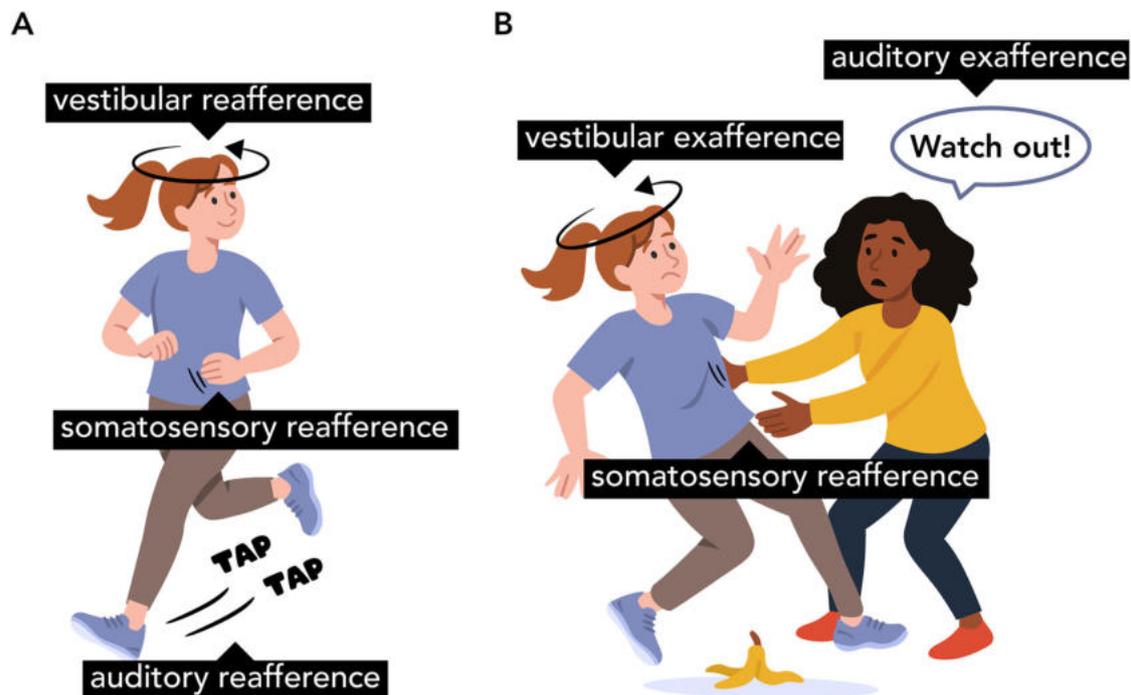
Figure 1. All organisms need to differentiate between sensory input produced by voluntary movements and sensory input originating from external sources. **A**, While a girl is running, she hears her own footsteps (auditory reafference), feels the touch of her hands on her torso (somatosensory reafference), and receives vestibular input as she moves her head (vestibular reafference). **B**, The same girl hears her friend's voice calling her to be careful (auditory exafference), feels her friend's touch on her body to stabilize her (somatosensory exafference), and experiences vestibular input as she involuntarily falls after slipping on a banana peel (vestibular exafference).

that compares them with actual feedback. The result is an error signal that closes the loop by projecting back to update the predictions (Fig. 2A). In view of the multiple nested feedback loops making up the brain and the intricate ways they have evolved, the task of mapping these elements onto neuronal structures has been colossal. In mammals, a wide range of brain structures (neocortex, cerebellum, basal ganglia, superior colliculus, etc.) and their input systems (neuromodulatory systems, thalamocortical, climbing fibers, etc.) have been suggested to be the seat of either prior knowledge or comparison. The effect of prediction signals, often considered to enact mathematical operations like "subtraction," "filtering" (Bays and Wolpert, 1993; Bays et al., 2006; McNamee and Wolpert, 2019), or "optimal combination" (Körding and Wolpert, 2004), has been variably described as "cancellation," "suppression," "gating," "attenuation," "adaptation," or "integration," among other terms.

The neuronal systems mentioned so far predict sensory consequences of movement and compare them to sensory feedback at high temporal precision. The result is a cancellation of the reafferent (i.e., self-generated) part of sensory signal flow (RA in Fig. 2B). As we will discuss, this cancellation may also involve processes that begin even before the reafferent input is received, indicative of predictive processing. In this review, we will refer to this cancellation as "reafference attenuation." The Cullen lab has been investigating how reafferent vestibular signals are attenuated by active head movements in monkeys. The Schwarz lab has focused on the attenuation of reafferent tactile signals during reach movements in the rodent whisker system, while the Kilteni lab has explored the attenuation of reafferent tactile signals in the human somatosensory system. The Schneider lab has studied auditory reafference attenuation during locomotion and other movements in rodents.

A second aim of this review is to discuss whether there exist separable neuronal systems that, in addition to reafference

attenuation, suppress the flow of sensory signals during movement. Often the effects of these neuronal systems have been studied under the name of "sensory gating" or "sensory suppression" (Ghez and Lenzi, 1971; Chapin and Woodward, 1981; Rushton et al., 1981; Williams et al., 1998; SG in Fig. 2B). Sensory gating typically shows a looser relationship to kinematic details of movements than reafference attenuation, often starting before and/or lasting longer than the movement. We understand sensory gating as a suppression of sensory flow that reaches beyond the attenuation of reafferent signals and also affects exafferent ones (i.e., externally generated). Sensory gating is observed in cortical motor or parietal areas and affects subcortical stages via corticofugal processes including the brainstem and the spinal cord. The term gating implies the binary operation of an on/off switch. Cullen and colleagues have studied a gating system in which one motor system transiently shuts down the sensory feedback generated via activation of another motor system to prevent counterproductive functional effects—suggesting a mechanism that is close to binary in nature (Fig. 2B, "SG, non-predictive"). In contrast, studies in other sensorimotor systems suggest more graded forms of sensory suppression. Research by Schneider and colleagues in the auditory domain, along with data from Schwarz and colleagues, as well as Kilteni and colleagues in the tactile domain, shows that sensory suppression is often incomplete. These studies propose that sensory suppression may adapt signal flow in a graded way to contextual parameters (Fig. 2B, "SG, different predictive target"). Thus, the term sensory gating as discussed here, already points to a class of systems, rather than a unique design fitting all purposes.

We are well aware that prediction targets can widely vary, including, among other things, sensory consequences, action outcomes (e.g., goals), or rewards. For purposes of clarity, from here on, we will use the term predictive in this article exclusively for processes that predict sensory consequences, i.e., specific
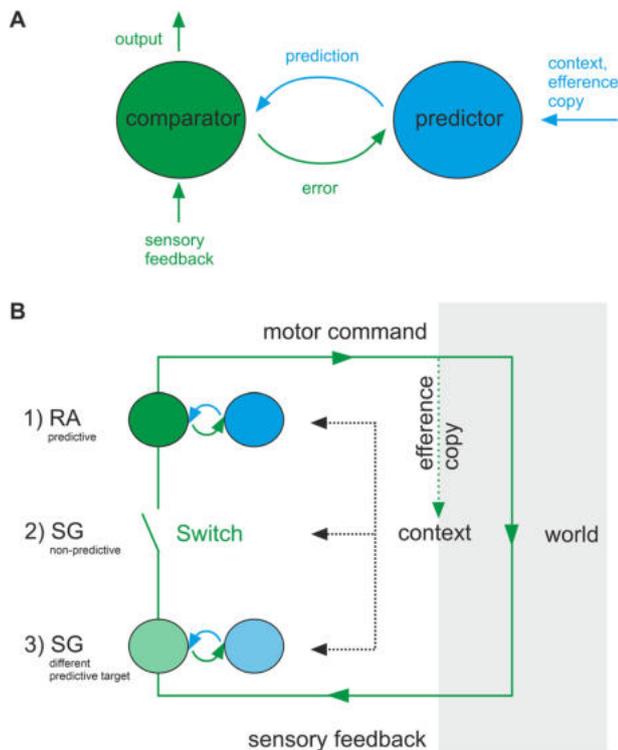
Figure 2. *A*, Predictive loop consisting of a predictor and a comparator. Predictions based on learned action–feedback associations (blue) are compared with actual sensory feedback (green). The resulting discrepancy (error) is used to update the associations of the predictor (shown) or the motor command (not shown). The predictor is informed by context and the efference copy. *B*, Possible interaction between reafference attenuation (RA) and sensory gating (SG) systems as discussed in this review. A sensorimotor loop is illustrated, in which a motor command generates an action in the world, which in turn leads to sensory feedback. (1) Reafference attenuation (RA). (2) Sensory gating (SG) functions as an ON/OFF switch, triggered either by another sensorimotor system to avoid detrimental interactions (e.g., interaction between the saccade and VOR systems; see the gating section) or by broader nonpredictive contextual factors (e.g., backward masking in human hand movements; see the gating section). (3) SG can also be understood as another class of predictive system, targeting a different prediction outcome (reward, distance to target, etc.) than sensory consequences (e.g., sensory gating in tactile and auditory systems; see the gating section).

features (e.g., frequency, location, intensity) within the same sensory modality, rather than merely reflecting a general, time-locked modulation associated with movement execution. We will discuss whether sensory gating constitutes a predictive system in its own right or instead merely suppresses sensory signals in a nonspecific, nonpredictive way.

Attenuation of Sensory Consequences of Current Action (Reafference Attenuation)

The process of attenuating predicted sensory consequences extends in similar ways to all senses (Fig. 1). Head or whole-body movements generate vestibular consequences, while nearly all body movements engage tactile and auditory consequences. These reafferent signals overlap with concurrently received external inputs, making it challenging to distinguish between the two. As we will discuss below, reafferent signals can be predicted based on motor-related information and eliminated from sensory flow by attenuating the responses to the self-generated input. We will discuss differences in brain structures involved in different species and sensory modalities and the interaction of different attenuation systems in different sensorimotor loops.

Evidence from vestibular studies in nonhuman primates

In the vestibular system of primates, vestibulospinal and vestibulo-collic reflexes provide robust postural responses to unexpected disturbances by stabilizing the head relative to space. However, if these reflexes were engaged during voluntary behaviors—such as walking or turning the head—they would counteract the intended movement and interfere with the goal of moving through space. A similar reasoning applies for perception. A lack of reafference attenuation would make it difficult to determine whether the body or the environment is moving. Reafference attenuation thus provides a unifying solution to a fundamental problem: how to maintain motor precision and perceptual clarity while navigating a dynamic environment.

To implement this distinction, vestibular reafference is substantially attenuated at the first central stage of processing, in a specific population of vestibular-only (VO) neurons within the vestibular nuclei. Single-unit recordings have demonstrated that VO neurons (but not the presynaptic vestibular afferents; Cullen and Minor, 2002; Jamali et al., 2009; Mackrous et al., 2022) show sharply reduced responses during self-generated movements—including head rotations (Roy and Cullen, 2001, 2004), translations (Carriot et al., 2013), static changes in head orientation (Mackrous et al., 2019), and multidimensional movements (Carriot et al., 2015)—while remaining responsive to unexpected, externally imposed motion. Because VO neurons provide the main vestibular input to vestibulospinal and vestibulo-collic reflex pathways, their suppression during active motion prevents inappropriate reflex engagement that would counteract voluntary movement.

Notably this reflects a highly specific form of reafference attenuation: sensitivity to vestibular reafference is attenuated while that to exafference preserved even when both occur simultaneously (Roy and Cullen, 2001; Brooks and Cullen, 2014). Experiments in which monkeys made voluntary head movements while a vestibular platform applied counteracting passive motion revealed that cancellation in VO neurons was only observed when "proprioceptive" feedback matched the predicted consequences of the motor command (Roy and Cullen, 2004). When this match was disrupted—for example, by activating neck muscles while the head was immobilized—suppression was abolished [reviewed in Cullen and Zobeiri (2021)]. Notably, this selective vestibular reafference attenuation has been observed across species—including in mice as well as both Old World and New World monkeys—highlighting its evolutionary fundamental role in vestibular processing [reviewed in Cullen (2019)].

Recent work has established that the internal model required for vestibular reafferent cancellation depends on a cerebellar computation that compares actual vestibular input to an internal prediction of expected sensory consequences (Cullen and Brooks, 2015). This prediction is generated by Purkinje cells in the anterior vermis, which integrate sensory and motor-related signals to estimate the outcomes of voluntary movement (Zobeiri and Cullen, 2022, 2024). When the predicted and actual feedback match, these Purkinje cells send inhibitory projections to the vestibular and deep cerebellar nuclei to cancel VO neuron response to vestibular reafference, thereby preventing reflex pathways such as the vestibulo-collic and vestibulospinal tracts from counteracting voluntary movement. A population of ~40 Purkinje cells is sufficient to mediate this cancellation during self-generated head motion. When a mismatch occurs—such as during novel or unexpected conditions—the cerebellum signals this discrepancy, allowing for adaptive recalibration of motor output.

Similarly, self-generated vestibular signals are attenuated in the ascending thalamocortical pathway, extending the effects of cerebellar suppression beyond reflex circuits. This attenuation arises because thalamic neurons receive direct input from VO neurons, whose activity is selectively suppressed during voluntary motion. As a result, neurons in the ventral posterior lateral thalamus show over 80% reduced activity during active compared with passive head movement (Dale and Cullen, 2019). Like VO neurons, they respond selectively to passive motion even when active and passive movements occur simultaneously. Thus, cerebellar modulation of VO output shapes both reflexive motor responses and ascending vestibular signals. This shared, prediction-dependent mechanism ensures that both motor and perceptual pathways remain sensitive to unexpected stimuli while filtering out predictable, self-generated input [reviewed in Cullen and Chacron (2023)].

Attenuation in VO neurons only occurs when proprioceptive feedback confirms the predicted consequences of a motor command, ensuring that suppression is both context-dependent and precise. Because VO neurons contribute to both brainstem reflex circuits and ascending thalamocortical pathways, their modulation by cerebellar output shapes motor and perceptual processing in parallel. In this way, cerebellar-mediated attenuation of vestibular reafference implements a core multisensory mechanism—one that filters predictable self-motion signals while preserving responsiveness to unexpected stimuli, thereby enabling perceptual clarity and motor precision during active behavior.

Evidence from somatosensory studies in humans and rodents
In human studies, somatosensory reafference attenuation has been primarily focused on perception. A large body of psychophysical research has consistently shown that self-generated touches are perceived as weaker and/or less ticklish than externally generated ones of identical intensity [Blakemore et al., 1999; Shergill et al., 2003; Bays et al., 2005; Kilteni and Ehrsson, 2017, 2022; reviewed in Kilteni (2023)]. These attenuation effects have been observed across the human lifespan (Wolpe et al., 2016; Timar et al., 2023) and are attributed to participants' predictions about the upcoming reafferent input (Bays et al., 2006; Job and Kilteni, 2023; Cemeljic et al., 2025; Valè et al., 2025). Critically, previous studies have shown that somatosensory reafference attenuation requires motor intention (Kilteni et al., 2018) and is not present during passive movements (Kilteni et al., 2020). Temporal prediction errors, that is, mismatches between the predicted time of self-generated input and the time of the received afferent input reduce perceptual attenuation, consistent with the predictive nature of the mechanism (Blakemore et al., 1999; Kilteni et al., 2019).

At the neural level, neuroimaging studies have confirmed these behavioral findings: the contralateral primary (Hesse et al., 2010; Job et al., 2025) and bilateral secondary (Blakemore et al., 1998; Kilteni and Ehrsson, 2020; Job et al., 2025) somatosensory cortices show reduced activation during self-generated touch compared with externally generated touch, even if both touches have identical intensity. Moreover, reduced cerebellar activation has also been observed under the same conditions (Blakemore et al., 1998; Kilteni and Ehrsson, 2020). Consistent with the psychophysical observations, temporal errors between the predicted time of self-generated input and the time of the received afferent input increase the somatosensory and cerebellar activation, indicating reduced neural attenuation (Kilteni et al., 2023).

Increased functional connectivity between the cerebellum and the somatosensory cortex has been observed during self-generated touch compared with externally generated touch, leading researchers to propose that this coupling reflects the predictive signal responsible for attenuating the somatosensory reafference (Kilteni and Ehrsson, 2020). Supporting this interpretation, cerebello-cortical connectivity is reduced when temporal mismatches are introduced between the predicted time of self-generated input and the time of the received afferent input (Kilteni et al., 2023). Notably, neuroimaging studies with higher temporal resolution have shown that this increased connectivity occurs prior to the arrival of the reafferent input (Job et al., 2025), providing further evidence that the cerebellum contributes to predictive attenuation by modulating somatosensory processing in advance of expected sensory consequences.

While human studies have provided compelling evidence for both perceptual and neural mechanisms of somatosensory attenuation, the rodent whisker system, known for the simplicity of its generated movement and accessibility of neuronal bases, offers a unique opportunity to dissect the cellular and circuit-level mechanisms underlying tactile processing and active touch (Feldmeyer et al., 2013). However, measurements of sensory feedback with whisking in air have revealed that tactile flow does not contain information about whisker kinematics, and therefore it is difficult to control experimentally (Khatri et al., 2009). This is the reason that the study of movement-related modulation of tactile flow (aka whisker "active touch") has been limited so far to sensory gating (discussed in the section about sensory gating).

To identify whether the whisker tactile system as well houses neuronal mechanisms of somatosensory reafference attenuation, mice executing a whisker reach task were presented with learned tactile consequences that were experimentally introduced either in the form of whisker flicks (after blockade of motoneurons to the whisker muscles, "open loop") or as electrical stimulation on the ascending tactile pathway on the level of the principal trigeminal nuclei ("closed loop"). The results from both experiments showed that reafference attenuation manifests itself as a rapid attenuation of sensory responses within an interval of ∼50 ms around the onset of the learned sensory consequence. Omitting the learned stimulus generated a "prediction" signal, an inhibitory response (Gupta et al., 2023), like the one seen by Bell (1982) in his famous studies of reafference attenuation in weakly electric fish. Reafference attenuation in the whisker system, so far, has been measured solely in the primary somatosensory cortex. Future questions include the role of the cerebellum to generate the reafference attenuation and the anatomical and functional assessment, where on the ascending tactile pathway, attenuation is first introduced.

Evidence from auditory studies in mice
Movement signals engage the auditory system during a variety of behaviors and at all levels of the neuraxis (Müller-Preuss and Ploog, 1981; Schneider et al., 2014; Zhou et al., 2014; Williamson et al., 2015; Yang et al., 2020; Morandell et al., 2024). Even at the earliest stages of auditory processing, movement modulation of auditory activity is sensitive to acoustic features, reflecting a predictive component. For example, neural responses to a mouse's own licking sounds are attenuated in the auditory brainstem, and the magnitude of this auditory reafference attenuation can scale with loudness (Singla et al., 2017). Movement signals acting at the level of the cortex appear to be particularly malleable and useful for predictive processing (Schneider and Mooney, 2015, 2018; Schneider, 2020). In humans, monkeys, and mice, auditory cortical responses to predictable self-generated sounds are weaker than are responses to

the same sounds heard passively or self-generated sounds that deviate from expectation (Eliades and Wang, 2008; Keller and Hahnloser, 2009; Flinker et al., 2010; Rummell et al., 2016; Schneider et al., 2018). This predictive attenuation of reafferent sounds can be observed at the level of neural populations, single neurons, and perception (Schneider et al., 2018; Audette et al., 2022; Audette and Schneider, 2023; Zhou and Schneider, 2024).

In addition to producing weak responses to sounds that match expectation, some auditory cortex cells carry signals resembling sensory prediction errors pointing to a comparator function within the auditory cortex (Fig. 2A). These prediction-error neurons are not responsive to passive sounds, to silent movements, or to movements that produce an expected consequence. Instead, they are active only when a movement makes an unexpected sound (Audette and Schneider, 2023). Different groups of the auditory cortex cells are responsive to different acoustic errors, indicating that the auditory cortex encodes rich error-related information that could be useful for learning and guiding behavior.

The auditory cortex also receives predictive signals. When mice expect to hear a sound at a particular phase of a behavior, movement-responsive neurons in the auditory cortex increase their activity, building up and peaking around the expected time of the sound—even if the sound is omitted (Audette et al., 2022). Moreover, when a movement is expected to produce a sound of a particular frequency, movement-responsive neurons tuned to that frequency show stronger responses than those not tuned to it (Schneider et al., 2018; Audette et al., 2022). These predictive signals tend to be concentrated in deep cortical layers, consistent with input from motor sources including the motor cortex, basal ganglia, and basal forebrain (Audette et al., 2022; Zhou and Schneider, 2024).

What are the circuit mechanisms that give rise to this predictive auditory reafference attenuation? While cerebellar-like circuits are the most well studied for learning and using internal models for predictive processing, cortical circuits are also well suited for flexible, context-specific processing and the integration of motor, sensory, and modulatory signals (Schneider, 2020). The auditory cortex receives input from motor and neuromodulatory centers, both of which are active during behavior (Nelson et al., 2013; Nelson and Mooney, 2016; Clayton et al., 2021). A substantial fraction of motor-related activity in the auditory cortex arises from long-range inputs from the motor cortex (Schneider et al., 2014). The motor cortex cells that project to the auditory cortex are active during movements including locomotion and forelimb behaviors (Schneider et al., 2018; Holey and Schneider, 2024). Interestingly, these neurons are also sensitive to sound and are modulated by expectation and error, suggesting that the motor inputs to the auditory cortex might already contain information above and beyond ongoing behavior (Holey and Schneider, 2024). Although movement-related signals in the auditory cortex can encode expectation-related information, it remains unknown whether motor inputs to the auditory cortex convey an expectation per se or whether they convey only movement information, which is transformed into an expectation locally within the auditory cortex (Leinweber et al., 2017; Zhou and Schneider, 2024). Ongoing work aims to understand whether the forward model for sound-behavior predictions resides in the auditory cortex, motor cortex, or some combination of the two.

Interim conclusion
Together, evidence from the vestibular, somatosensory, and auditory systems suggests that the brain uses predictive mechanisms to attenuate reafferent (i.e., self-generated) sensory input, thereby supporting accurate perception and motor control. While the circuits of this sensory reafference attenuation differ—ranging from cerebellum-dependent pathways to cortical modulation—a shared principle emerges across species and modalities: motor signals suppress expected sensory consequences, enhancing sensitivity to unexpected external events.

Gating of All Sensory Input during Action (Sensory Gating/Suppression)
We now turn to a second system of interest, that of sensory gating, also called sensory suppression. The difference to reafference attenuation is that sensory gating also affects exafferent sensory signals. As we will discuss below, in contrast to the predictive reafference attenuation, the predictive nature of sensory gating remains unclear and appears inconsistent across species and modalities. We will discuss differences in brain structures involved in different species and sensory modalities.

Evidence from vestibular studies in nonhuman primates
The vestibular nuclei contain two primary classes of neurons that receive direct input from vestibular afferents and support distinct functional pathways. One class are VO neurons that project to spinal and thalamic targets and exhibit suppressed responses during active self-motion, as reviewed in the reafference attenuation section above. In contrast, a second class of central vestibular neurons—those mediating the vestibulo-ocular reflex (VOR)—also receives direct afferent input but preserves their responses to vestibular reafference during active self-motion (Roy and Cullen, 1998, 2002). This preserved encoding is essential: the VOR must remain active to generate compensatory eye movements that stabilize gaze during natural head movements. Suppressing reafferent input in this context would undermine visual stability, particularly during locomotion when head motion is continuous and dynamic.

Although VOR pathway neurons preserve vestibular reafference during active self-motion—ensuring gaze remains stable relative to space—this pathway is transiently gated when the behavioral goal is to redirect gaze rather than stabilize it. This form of gating does not align with the definition of prediction provided in Introduction—namely, a process in which internal models compute specific sensory consequences of an action, compare them with actual feedback, and use any resulting error to update future predictions. In contrast, the gating of VOR pathway neurons does not involve such a comparison or error-based updating. Instead, this general suppression is mediated by a mechanism that is engaged during saccadic eye movements to act on both reafferent (self-induced head movement during gaze shift) and exafferent vestibular inputs [externally induced head rotation to induce VOR; reviewed in Cullen and Roy (2004)]. It therefore complies with the definition of sensory gating used here, which demands that the suppression effects exafferent signals. Notably, during active head movements, the timing of this gating is tightly locked to the duration of the saccade itself, not the head movement and associated vestibular reafference—underscoring that it is driven by the eye movement command rather than predictive processing.

Specifically, during active coordinated eye–head gaze shifts and pursuit, brainstem saccade-generating circuits briefly inhibit the VOR pathway neurons (Roy and Cullen, 1998, 2002, 2003). In the case of gaze shifts, this suppression is provided by premotor burst neurons in the pontine paramedian reticular formation,

which drive rapid eye movements via direct projections to ocular motoneurons and send a collateral inhibitory drive to the vestibular nuclei [reviewed in Cullen and Roy (2004)]. This projection transiently suppresses the VOR pathway, preventing it from generating compensatory eye movements opposite to the intended shift. Notably, suppression of the VOR pathway is precisely time-locked to gaze shifts and is most pronounced at their onset, with VOR neuron sensitivities gradually recovering by the end of the movement (Cullen et al., 2004). This switch-like mechanism ensures that gaze redirection is not counteracted by the reflex and underscores the task-specific modulation of vestibular pathways.

Together, these findings highlight that the vestibular system does not rely on a global gating strategy. Instead, it exhibits pathway-specific modulation tailored to the functional demands of each circuit. Suppression of predictable, self-generated signals is selectively applied, enhancing sensitivity to unexpected events in postural and perceptual systems, while preserving continuity and precision in pathways critical for gaze stabilization. Notably, this modular organization stands in contrast to classical models of sensory gating and reveals the specialized computations that support stable behavior during active movement.

Evidence from the rodents' whisker system

Sensory gating in the whisker-related somatosensory system is a phenomenon where sensory responses are attenuated during or around the time of self-initiated movement. It is reflected by a general suppression of all tactile flow during a whisker movement as compared with the same tactile input during rest (Hentschke et al., 2006; Ferezou et al., 2007). The modulation is of central origin, as blockade of primary afferent activity does not abolish gating in upstream tactile pathways (Hentschke et al., 2006). Moreover, gating involves corticofugal projections—descending signals from the cortex that influences subcortical sensory relays (Seki et al., 2003; Chakrabarti and Schwarz, 2018). Two important properties of sensory gating in the whisker system is that it is active even during learned whisks aimed at touching a moving target that predicts reward and that it is independent from the kinematic state of the whisking movement (Hentschke et al., 2006; Gupta et al., 2023). The idea that only irrelevant sensory signals are gated, as suggested for primate grasping movements [Juravle and Deubel, 2009; Juravle et al., 2010; Saradjian et al., 2013; Colino et al., 2014; but see (Debats et al., 2016)], is still an open possibility as it was found that parallel ascending tactile channels in the whisker reach system are differently affected by gating (Chakrabarti and Schwarz, 2018). Moreover, the presence of gating during a comparatively simple reach movement did not point to an interaction of two specific sensorimotor systems as discussed above for the primate head movement system.

In summary the function of sensory gating is still unclear. This has led to diverging explanations of gating being either related to "higher" brain function, i.e., triggered by cognitive or attentional processes, or in stark contrast, as belonging to reafferent attenuation (Juravle et al., 2017). At first glance, sensory gating and reafferent attenuation might appear to be different manifestations of the same underlying process, since both modulate sensory input based on motor activity. An important aim, therefore, is to show the existence of both systems and delineate them in terms of behavioral function and neuronal mechanisms. The approach using a whisker reach task in mice (Gupta et al., 2023) exploited the fact that reafference attenuation is temporally precise, while sensory gating is effective during the whole movement, extending even to a period of time before and after the movement. Head-fixed mice were trained to move their whisker from a starting point A

to a target B to gain a water reward. During and after that movement, a defined sensory stimulus was presented, either as a whisker flick during the motor command destined for the immobilized whisker or as an electrical stimulus in the trigeminal nuclei during actual movement. The stimuli were of two classes, one presented at a fixed learned delay from motor command onset and the other at arbitrary nonlearned delays. The responses to both stimuli were compared with a stimulus of identical intensity presented at whisker rest. Recording from neurons in the primary somatosensory cortex, it was observed that both stimuli gave a separable amount of suppression of the tactile response: when the stimulus was shifted away from the expected timing of the self-generated movement, attenuation related to state estimation disappeared, but that of sensory gating remained. At the predicted time of the arrival of the tactile consequence, a negative response was identified by stimulus omission—similar to classic findings in weakly electric fish (Bell, 1982). These experiments show for the first time that neuronal correlates of sensory gating and reafference attenuation can be measured and separated in one and the same experiment. These observations align with and complement Kilteni and Ehrssons's behavioral result in humans (2022). Sensory gating as explored so far does not align with movement kinematics or timing and therefore would be classified as nonpredictive in the sense of the term we use it here. However, it remains an open question whether other prediction targets, like movement outcome or reward, play a role for its activation.

Evidence from somatosensory studies in humans

In humans, sensory gating has been shown in terms of reduced sensitivity (e.g., in reduced detection rate or precision) to externally generated touches both during and before voluntary movement (Chapman et al., 1987; Williams and Chapman, 2000; Chapman and Beauchamp, 2006; Cybulska-Klosowicz et al., 2011; Voudouris et al., 2019) compared with rest. Electrophysiological studies have shown that these gating effects are due to an inhibition of somatosensory-evoked potentials during active movement, as compared with rest, at both subcortical and cortical levels of the somatosensory pathway (Rushton et al., 1981; Chapman, 1994; Lei et al., 2018). Similar tactile gating effects have been observed in cats (Ghez and Lenzi, 1971), rats (Chapin and Woodward, 1981), and nonhuman primates (Seki and Fetz, 2012).

It is important to note that, in contrast to the somatosensory reafference attenuation, gating effects appear less specific as they tend to manifest for all somatosensory input, both reafferent and exafferent (Rushton et al., 1981; Kilteni and Ehrsson, 2022). Moreover, its relationship with sensorimotor predictive mechanisms has been questioned by the fact that gating effects have been repeatedly documented during passive movements, both electrophysiologically (Rushton et al., 1981) and behaviorally (Chapman et al., 1987; Williams and Chapman, 2002; Chapman and Beauchamp, 2006). This has led to the suggestion that movement-related gating or suppression is, at least in part, explained by nonpredictive mechanisms. Specifically, sensations arising from the muscles, joints, and skin of the moving limb may mask externally generated tactile stimuli applied to that limb, doing so in a backward-acting, postdictive manner that affects the perception of earlier stimuli (Williams and Chapman, 2002). Given the findings of gating during passive movements (i.e., in the absence of motor commands), it is plausible that sensory signals from the passively moving limb can also mask exafferent touches. This mechanism may account for the lack of significant differences in gating between active and passive movements (Chapman et al., 1987; Williams and Chapman, 2002).

Evidence from auditory studies in mice

In addition to contributing to predictive processing, movement signals in the auditory system provide a potent form of sensory gating typically leading to weaker sound-evoked responses during movement compared with rest. During locomotion and other behaviors, spontaneous and sound-evoked activity is suppressed in the inferior colliculus, auditory thalamus, and auditory cortex (Schneider et al., 2014; Williamson et al., 2015; Rummell et al., 2016; Reznik et al., 2021). Movement-related changes in auditory activity typically occur before movement onset and are present even in the absence of sensory feedback, consistent with a motor origin as opposed to being driven by sensory reafference (Schneider et al., 2018; Audette et al., 2022). Humans and mice report that sounds heard during movement are weaker than those heard during rest, providing a perceptual correlate of this sensory gating during behavior (Schneider et al., 2018; Buaron et al., 2020). While being nonpredictive for temporally precise sensory consequences, as defined here, this auditory gating coincides with the onset and duration of movements. It is therefore an open question whether it could have a prediction target beyond the prediction of sensory consequences. For example, life experience may teach animals that movements tend to make noise. Suppressing the auditory system during movement may therefore be both advantageous and adaptive, effectively turning the volume knob down during moments that are expected to be louder.

A remaining unresolved question is whether predictive auditory reafference attenuation and sensory gating in the auditory cortex are driven by the same or different circuit mechanisms. Some lines of evidence point toward a conserved mechanism. For example, both predictive attenuation and gating in the auditory system involved inhibition mediated by the recruitment of local inhibitory cells (Schneider et al., 2014, 2018; Zhou et al., 2014). Moreover, the motor cortex appears to be important for both gating and attenuation gain control and predictive processing, suggesting that the mechanisms might be at least partially overlapping (Schneider et al., 2014, 2018; Zhou and Schneider, 2024). As such, it is possible that the circuit mechanisms for generic sensory gating are malleable and can be shaped by experience, thus resulting in a form of suppression that is predictive and acoustically selective.

Alternatively, these two forms of movement modulation may arise through largely independent mechanisms. In addition to inputs from the motor cortex, the auditory cortex also receives input from other motor structures (e.g., basal ganglia) and strong cholinergic input from the basal forebrain (Nelson and Mooney, 2016; Clayton et al., 2021). Cholinergic and motor inputs converge on many of the same neurons but have different effects on auditory cortical activity (Nelson and Mooney, 2016). Neuromodulatory inputs may be better positioned to convey a gross modulatory signal that drives sensory gating, whereas cortical inputs may be more sensitive to experience and could mediate a predictive component. In the auditory system, it remains unresolved as to whether reafference attenuation and gating gain control arise from similar or distinct mechanisms.

Interim conclusion

Together, sensory gating is characterized by the broad suppression of both reafferent and exafferent sensory signals during movement and emerges as a distinct and widespread phenomenon that is functionally and mechanistically separable from reafference attenuation. Unlike reafference attenuation, which is temporally precise and predictive of specific sensory consequences, sensory gating tends to be less specific, lacking a clear temporal alignment with movement, and is present even during passive movements in some cases. Current evidence supports the view that sensory gating reflects a nonpredictive mechanism aimed at regulating sensory input more globally during movement.

Discussion

This review considered two classes of feedback loops that evolved in the mammalian brain, focusing on those that are tightly coupled to movement and suppress sensory signals. We maintain that two classes of mechanisms can be delineated by which the brain modulates sensory input during movement: reafference attenuation and sensory gating. While both reduce sensory inflow, they differ in specificity, timing, and underlying neural mechanisms. Reafference attenuation relies on predictive internal models to selectively suppress the expected sensory consequences of self-generated actions. In contrast, sensory gating reflects a broader suppression—less specific, often extending before and after movement.

We acknowledge that our definition of prediction, as prediction of sensory consequences, is limited and does not encompass predictions about exafferent stimuli, such as sensory-based expectations or reward predictions. However, all authors deemed this operational definition appropriate given the focus of the present review on sensorimotor processing.

Already at this point we can make out brain structures and processes that are more complex than just two different algorithmic principles. Reafference attenuation may often involve the cerebellum or cerebellum-like structures, but the neocortex may have its own mechanisms to compute similar signals. It is a future goal to find differences in algorithmic detail, memory storage, and behavioral function of different systems of reafference attenuation. Likewise, our examples reveal that sensory gating is likely not a unique algorithmic process. It can be highly specific, based on motor commands, to block one sensorimotor system in case of conflict with another. On the other hand, it may do the same thing in unspecific ways or may be part of predictive systems that deal with predictive targets different from sensory consequences of movement. These details are empirical questions for future research.

Functionally, these movement-related modulations may reflect the adaptive value of sensory prioritization. For example, somatosensory reafferent and vestibular inputs are attenuated thereby increasing the salience of externally generated touches and unexpected self-motion. Similarly, auditory input is often gated during locomotion, while the visual input is enhanced to support spatial orientation. This selective modulation supports the hypothesis that hierarchically nested predictive loops in the brain adaptively control sensory flow depending on behavioral goals.

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