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Current Opinion in Neurobiology

# A shared predictive architecture in the sensory cortex for statistical and reward-based learning

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The sensory cortex is widely considered a feed-forward feature extractor whose stimulus-driven responses can be modified by context or experience. Recent work, however, suggests a richer role. In implicit, statistical learning, mismatch responses in primary auditory and visual areas point to a computation of sensory prediction errors. In explicit, reward-based learning, converging evidence shows that populations in the sensory cortex rapidly develop reward prediction activity, firing when an expected outcome would follow the stimulus. These results demonstrate that, alongside feature representation, the sensory cortex has another core function: prediction. This predictive role could, in principle, be implemented by one circuit motif: feed-forward drive to basal dendrites, distal input to apical tufts, and local disinhibition. When the distal input carries a sensory prediction, the sensory cortex computes prediction errors by directly comparing predicted (distal) with actual, feedforward drive. When it carries outcome information, the sensory cortex computes a prediction, without computing errors. We assemble the empirical foundation for this possibility drawn primarily from the auditory cortex, complemented by convergent results from other sensory cortices and then provide a roadmap to test this principle.

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**Current Opinion in Neurobiology** 2026, **98**:103178

This review comes from a themed issue on **Systems Neuroscience 2025**

Edited by **Robert Froemke**, **Máté Lengyel**, **József Fiser**, **Livia de Hoz**

For a complete overview see the Issue and the Editorial

Available online xxx

**https://doi.org/10.1016/j.conb.2026.103178**



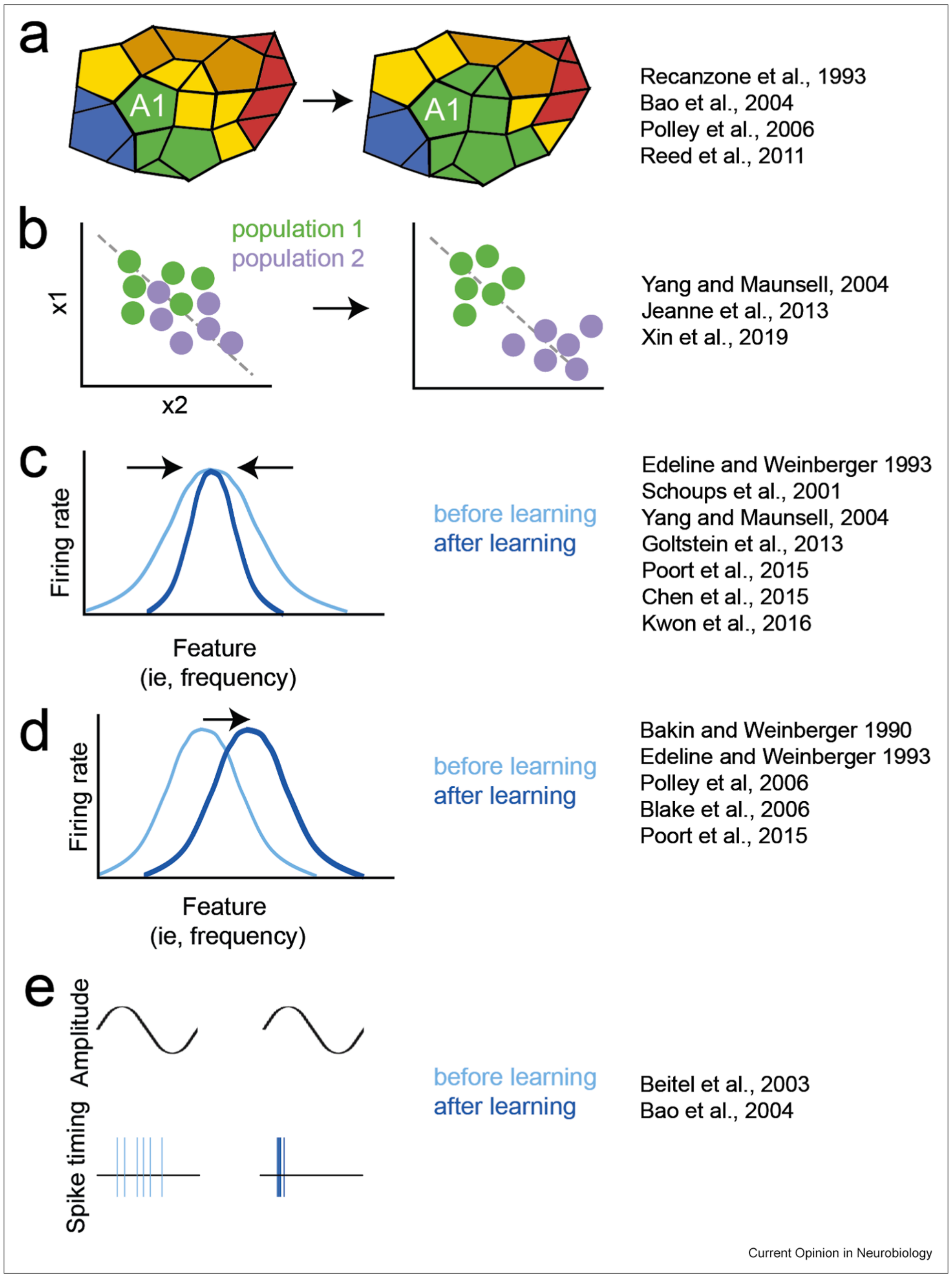
## Introduction

Traditional perspectives describe the sensory cortex as primarily encoding stimulus features, with progressively richer feature extraction occurring at subsequent stages of cortical processing. Seminal neurophysiological recordings established fundamental principles of feature encoding in the sensory cortex, initially suggesting limited plasticity post-development [1,2]. The subsequent introduction of awake, behaving animal preparations revealed substantial experience-dependent plasticity in the sensory cortex, with sensory representations reshaping as a function of learning [3,4]. Since then, the sensory cortex has been recognized to dynamically enhance representation of task-relevant features across sensory modalities (Figure 1). These changes in sensory representation are multiform: *topographic map plasticity*, where the representation of task-relevant features is expanded in the cortex to aid detection [4–7]; *reduced noise correlation* [8,9]; *sharpened tuning* to enhance single-neuron and population-level discrimination [8,10–15]; *shifts in receptive fields* [5,16,17]; and *increased phase-locking* for task-relevant frequencies [18,19]. These changes correspond to the perceptual demands of a given task-relevant feature, such as sound frequency or amplitude for audition [5].

Despite decades of evidence demonstrating learning-related plasticity in the sensory cortex, its fundamental computational role in learning remains unclear. Historically, how the sensory cortex facilitates learning has been examined in two broad, major categories: implicit or explicit learning. One prominent form of implicit learning is *statistical learning*, where humans and other animals incidentally extract regularities directly from sensory input. Explicit learning, by contrast, involves an element of goal-directedness. One widely studied example is discriminative *instrumental learning*, where sensory cues explicitly signal an action that leads to a desired outcome. A common feature of implicit and explicit learning is prediction: in implicit learning, animals acquire expectations about upcoming input, whereas in explicit learning, they predict which sensory information (and action pairing) will lead to specific outcomes.

Given that both forms of learning inherently depend on sensory processing, the sensory cortex likely plays a

**Figure 1**




**Types of learning-dependent plasticity of sensory-evoked responses.** (**a**) Topographic map plasticity in the primary auditory cortex. The sound frequency representation is denoted by color (blue to red: low to high frequency). The task-relevant frequency representation (green) expands with learning. (**b**) Illustration of improved population discrimination with learning. This enhancement can arise from multiple mechanisms, including changes in single-cell tuning and reductions in noise correlations across the population. (**c**) Sharpening of tuning; light blue denotes pre-learning; dark blue denotes post-learning. (**d**) Receptive field shift towards the learned feature. (**e**) Increased temporal fidelity, where individual neurons fire more reliably to onset of an amplitude modulated, pulsed stimulus.

crucial yet potentially overlapping role in each. A large body of work shows that sensory cortices process information in a predictive manner, with evidence for prediction suppression [20,21] and deviance detection [22–24]. In behaving animals, neural signatures of reward prediction [25–27] and self-generated sensory prediction [28] —prediction of a stimulus that results from an animal's own actions—further suggest that multiple forms of prediction may be implemented within the same cortical locus.

Here, we synthesize behavioral and physiological evidence that the sensory cortex supports both sensory and reward prediction and argue that a shared circuit motif underlies both. We advance a unifying claim: a conserved apical-tuft 'prediction gate' expresses different predictive operations depending on the content of the distal input. When distal input contains sensory information, the cortex compares it with feedforward drive to yield a sensory-prediction error (SPE) locally; when it carries reward timing/value, the cortex computes (or amplifies and relays) reward prediction (RP) signals, while signed reward-prediction errors (RPE) are computed downstream. This framing links statistical and reward-based instrumental learning within a single microcircuit motif and leads to clear, testable distinctions developed below.

## Statistical learning

Statistical learning (SL) refers to the extraction of sensory regularities without explicit feedback. It is observed broadly across species, including humans, primates, rodents, and birds [29] (in humans [30]; non-human primates [31]; songbirds [32]; dogs [33]; chicks [34]). The timescale of SL ranges from rapid adaptation on the scale of seconds or minutes [35] to ontogenetic processes like language acquisition, which unfolds over months to years [30]. In humans, statistical learning has been demonstrated to influence perception across modalities (for a review, see Ref. [36]) and decision-making through integration of regularities over experience [37].

Neural signatures such as stimulus-specific adaptation (SSA) and mismatch negativity (MMN) illustrate how the sensory cortex continuously filters the sensory stream and updates expectations based on local deviations. SSA, particularly well characterized in the auditory cortex, reflects the adaptation of stimulus-evoked responses to a frequent stimulus ('standard') and enhanced responsiveness to unexpected stimuli ('deviant') [22,38]. This leads to a form of sensory prediction error which can be operationally defined as the difference in firing rate elicited by a stimulus when it is unexpected compared to when it is expected. These adaptive processes appear hierarchically organized along sensory pathways, becoming increasingly pronounced from midbrain structures to primary cortical areas (for a review see Ref. [39]). The sensory cortex appears central to encoding and computing **sensory prediction errors (SPE)** in SSA, potentially integrating predictions from higher-order areas and modulating subcortical processing through top-down feedback [40–42].

## Instrumental, reward-based learning

Instrumental, reward-based learning refers to the process by which animals learn to associate specific sensory cues with particular actions that reliably lead to desired outcomes. In discriminative instrumental learning, specifically, animals learn that certain stimuli (S+) signal which actions will produce rewards, while other stimuli (S−) indicate the absence or ineffectiveness of those actions. Successful performance on these tasks hinges critically on accurate sensory processing, as animals must first discriminate sensory cues before they can learn which actions yield rewards. Thus, the sensory cortex is centrally positioned to support this learning by representing and differentiating cues that guide adaptive behavior.

Historically, the dominant view held that the sensory cortex supports discriminative, instrumental learning by enhancing the sensory features that differentiate S+ from S−, thereby making the cue discrimination easier for downstream decision systems (Fig. 1). In auditory cortex this has been documented as receptive-field shifts toward the trained frequency, expanded map representation of task-relevant bands, tuning-curve sharpening, and enhancement of phase-locking (e.g., Refs. [5,6,15,18,19]). Parallel observations in visual cortex, including orientation-specific improvements and population-level sharpening with training, reinforce this "feature-enhancement" account [10–12]. Under this view, the computational contribution of the sensory cortex is to optimize the task-relevant feature representation, while valuation and action selection are computed elsewhere.

Seminal work has broadened this picture by showing that primary sensory areas can acquire **reward-prediction (RP)** activity during instrumental learning. In the primary visual cortex(V1), neurons come to fire at the expected time of reward following a visual cue [25], with later studies linking this to cholinergic-dependent mechanisms of temporal expectation [43]. Related phenomena have been reported outside vision; for example, neurons in the somatosensory cortex express reward-linked signals [44] that may track reward timing and choice. These studies established the existence of sensory cortical reward prediction signals and implicated long-range neuromodulatory inputs. What remained unresolved were two essential factors: 1) timing: do these signals precede or follow behavioral acquisition? 2) necessity**:** are they required for learning or merely epiphenomenal readouts of it? In short, do sensory cortical RP signals instruct learning, or do they simply reflect it once learning has occurred?

Addressing those open points, recent work shows that RP signals in mouse auditory cortex emerge rapidly within ∼20–40 trials as animals learn that an S+ tone predicts water after execution of an initial response [27]. The RP signal increases at the expected reward time rather than at tone onset, and it emerges even faster than what can be measured behaviorally. These data suggest that the RP signal in the auditory cortex emerges before, or concomitant with, behavioral acquisition (see Ref. [45] for a more detailed review). When reward was omitted on a fraction of S+ trials, reward prediction activity in the AC persisted, but no error signal was observed. This suggests that the **auditory cortex does not encode reward prediction error**, consistent with findings in the visual cortex where reward-timing activity was indistinguishable in rewarded and unrewarded trials [25]. Notably, causal perturbations confined to the RP timing within the trial (silencing auditory cortex during the reward-prediction epoch) delayed acquisition of the S+ action reward association [27]. Together, these results argue that the auditory cortex contributes instructive, temporally specific predictions that shape instrumental behavior, rather than merely improving cue discriminability. In other sensory domains (i.e., somatosensory, olfaction) reward-related signaling has been observed but the precise computation (reward itself, prediction or prediction error) has been harder to disentangle, perhaps due to a more integrated active sensing-motor loop such that departures from expected reward may exist in these sensory cortices [46,47].

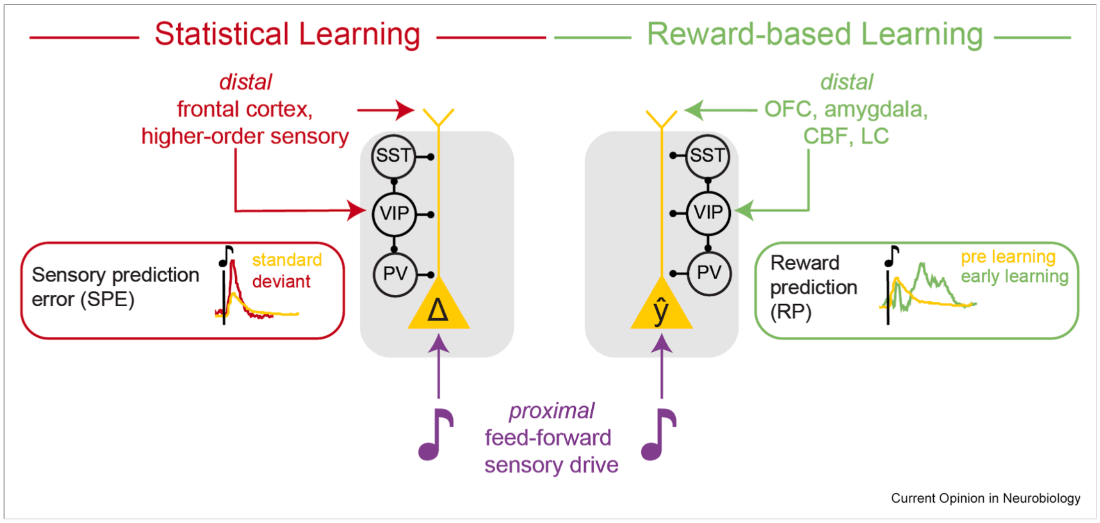
## Shared neural substrate for prediction

Primary sensory cortices share a conserved circuit substrate that could perform dissociable predictive operations. Thalamocortical afferents provide feed-forward drive to perisomatic and basal/proximal dendrites of pyramidal neurons (primarily layers 3–4), while long-range feedback from higher cortical areas terminates in superficial cortical layers onto apical tuft dendrites; this laminar motif is well documented across neocortex and in sensory areas specifically [48–51]. Neuromodulatory axons, notably cholinergic projections from basal forebrain, arborize densely in superficial layers and modulate excitability and plasticity, including in the auditory cortex. These projections directly modulate distinct interneuron subtypes (for a review see Ref. [52]). Within local inhibitory microcircuits, vasoactive intestinal peptide (VIP) interneurons transiently suppress somatostatin-positive (SST) cells (dendrite-targeting) and parvalbumin-positive (PV) cells (soma-targeting), creating brief windows during which apical–basal coincidence can generate tuft-initiated NMDA/$Ca^{2+}$ events (plateaus) and burst output [26,53–55]. Within this scaffold, we posit that the content carried by distal inputs and the presence of a local sensory reference determines the observable computation.

- **Sensory-prediction error (SPE):** When distal inputs convey information about the ongoing sensory stream (e.g., contextual or sequence expectations), coincidence with feed-forward drive can engage tuft-dependent dendritic spikes and brief bursts that report a local deviation between expected and received sensory input. This report serves as an SPE at the timescale of the incoming sensory input. Empirically, mismatch responses consistent with SPEs are observed in rodent auditory and visual cortices. VIP–SST dynamics participate in gating these mismatch responses [56–59].
- **Reward prediction (RP):** When distal inputs carry outcome-related signals, transient disinhibition of tuft dendrites could promote plateau-like depolarizations that are time-locked to the expected outcome. This activity constitutes a RP signal that could then be relayed for downstream evaluation in striatal–dopaminergic circuits, where the signed reward-prediction error is computed.

Each element of this implementation is supported by convergent evidence (Figure 2). 1) Paired apical–basal activation can trigger dendritic $Ca^{2+}$/NMDA spikes and promote potentiation at feedback synapses; in vivo and in vitro work across sensory cortices documents tuft-initiated plateaus and burst output as the readout of such coincidence [53,54]. 2) VIP interneurons specialize in disinhibitory control across the cortex (including auditory cortex), suppressing SST (and to a lesser extent PV) cells to open dendritic "windows" that facilitate pyramidal responses and associative plasticity; VIP/SST activity is differentially engaged around deviant stimuli [55]. 3) Orbitofrontal cortex top-down projections send cue-, delivery-, and omission-locked signals to auditory cortex, providing a cortical route for outcome-related information [60–62]; amygdalo-cortical and other frontal/associative projections also contribute affective and contextual signals. 4) Basal forebrain cholinergic axons modulate excitability and plasticity and can be rapidly recruited by reinforcement; in V1 they are required for the acquisition of reward-timing responses [43]. In mouse auditory cortex, basal-forebrain cholinergic axons deliver an *integrated signal* containing both sound-locked and value/state components into layer 1 [63], providing a direct, temporally-aligned pathway by which reinforcement context can couple to sensory timing at apical tufts. 5) Auditory corticostriatal neurons are potentiated during auditory discrimination learning [64,65], positioning the sensory cortex to broadcast RP signals which downstream basal ganglia and midbrain dopamine systems can compare to actual outcomes and compute signed prediction errors. Recent accounts suggest that the striatum is a potential candidate for providing a behaviorally-relevant expectation signal [66].

**Figure 2**




**Shared circuit motif for prediction in statistical and reward-based learning.** In both cases, cortical pyramidal neurons (yellow) receive proximal, feedforward sensory input (purple, here represented as a sound input). In Statistical Learning, distal input (red) from higher-order sensory and frontal cortices provides a sensory prediction signal (e.g., what sound is expected) to the apical tufts of sensory cortical neurons and the local inhibitory circuit (here schematized as direct input to VIP interneurons, black). The pyramidal neuron then directly compares the prediction (distal input) with the actual (proximal input) and computes an error signal (Δ). This leads to a sensory prediction error (SPE) shown as increased firing to rare deviant vs common standard sounds (red box). In Reward-based Learning, distal input (green) from cortical, subcortical or neuromodulatory regions provides a reward-related signal to the same microcircuit. Transient disinhibition of tuft dendrites at the time of the expected outcome, could support a late-in-trial reward prediction (RP) signal that co-exists, though remains uncoupled from, proximal sensory input.

In both instances of SPE and RP, correlated input to basal and apical dendrites can trigger an all-or-none plateau event in the apical tuft. These plateaus generate a large, branch-wide $Ca^{2+}$ signal that: (i) drives plasticity at the synapses which were recently active on that branch, which are mainly in L1, and (ii) biases somatic output towards burst firing. Analogous dendritic plateau-gated plasticity has been well documented in CA1 pyramidal neurons, where conjunctive proximal–distal input triggers plateau potentials that drive rapid, branch-specific synaptic changes and altered place-field representations [67]. Which of these consequences dominates—SPE or RP—depends on multiple factors, including the local circuit and neuromodulatory state. We propose that SPE plateaus primarily serve as a local teaching signal for plastic synapses in L1, whereas RP plateaus in corticostriatal neurons additionally generate strong bursts that broadcast a reward-prediction signal to downstream basal ganglia targets. In the case of SPE, a calcium plateau is sufficient for plasticity locally in L1, but because large, tonic changes in neuromodulatory tone (e.g., norepinephrine (NE) or acetylcholine (ACh)) are mostly absent, somatic burst firing would remain limited. The SPE events would not trigger a burst of spikes from the corticostriatal neuron and without an actual rewarded event, there will be little-to-no dopaminergic modulation in the striatum, and thus less striatal medium spiny neuron (MSN) firing. In the case of RP, higher levels of neuromodulation in the cortex (e.g., tonic NE and ACh) from vigilance and engagement amplify the consequences of the dendritic plateau, now triggering larger, high-frequency bursting from corticostriatal neurons. When coupled with the dopaminergic modulation in the striatum, this could influence basal ganglia loops involved in reward prediction error coding.

Taken together, these mechanisms support the view that a conserved microcircuit motif, including thalamocortical feed-forward drive, feedback onto apical tufts, neuromodulatory control of excitability/plasticity, and VIP-gated dendritic disinhibition, can express sensory prediction errors when context about the current sensory stream is available locally, and reward prediction when expected outcomes must be evaluated downstream, without requiring distinct anatomical or computational modules.

## Prediction as the unifying computation (sensory, outcome, and motor)

Stepping one level up from circuit mechanism, a single computation links the roles of the sensory cortex across implicit and explicit learning: prediction. Millisecond-scale SPEs arise when feedforward input deviates from feedback carried by apical tufts, as in SSA or MMN. Both the comparison (basal versus tuft inputs) and the resulting error signal can, in principle, be computed within the cortex itself. By contrast, RP signals become time-locked to expected reinforcement following a cue. The sensory cortex in this learning regime computes (or amplifies) a cue-locked expectation of reward and its timing, which downstream circuits then use to compute a signed reward-prediction error.

The generality of this computation and its proposed circuit implementation extend beyond sensory- and reward-related domains to motor prediction. During self-generated movements, primary sensory cortices form internal predictions of reafferent input, suppressing expected consequences and highlighting violations. In the auditory cortex, learned cancellation of self-produced sounds and feature-specific mismatch responses during active sensing have been demonstrated [28,68,69]. In the visual cortex, locomotion and eye-movement paradigms reveal V1 activity that encodes predicted optic flow and emits mismatch transients when visual consequences are perturbed [70,71]. These phenomena likely recruit the same laminar and microcircuit elements outlined above (layer-1 feedback conveying efference-copy or motor-context signals to apical tufts, apical—basal coincidence, and VIP-mediated disinhibition) supporting the view that the predictive operation is domain-general.

## Outlook

Here we describe a practical roadmap that outlines experiments that can support or break the proposed account by leveraging timing (SPE vs. RP), learning stage, and domain generality, with clear caveats to guard against alternative explanations.

### One preparation, two computations: leveraging when SPEs and RPs are generated

A powerful test of the framework is to measure and perturb SPEs and RPs in the same animal and task. The experimental handle is temporal: SPEs ride on millisecond-scale deviations between feed-forward drive and context (e.g., oddballs), whereas RPs are cue-locked but expressed at the expected time of reward.

A practical approach is a two-block design: first, a passive (or task-irrelevant) oddball sequence to quantify SPEs; second, a discriminative instrumental block with a fixed cue → reward delay to read out RPs as they emerge. With laminar recordings or two-photon dendritic imaging in auditory cortex, one can assay (i) superficial L1 activity and tuft events during both blocks, and (ii) VIP/SST dynamics as a local gate [26,56,58,59]. Causally, brief, trial-locked perturbations of L1 input (feedback and neuromodulation) or VIP ↔ SST balance should reduce mismatch bursts during oddballs and attenuate reward-timed events during learning, with minimal effects on early feed-forward feature responses [57,58,72,73].

To disentangle what the cortex verifies locally (i.e., error-generating) from what is evaluated downstream (i.e., prediction alone), as well as to identify the type of predictive processing at play, one could introduce unexpected sensory inputs (by altering stimulus features or omitting them) or unexpected rewards (by shifting their timing or omitting them), while monitoring activity in the relevant cellular compartments of the same animal. Particular attention must be paid to the statistical structure of expected versus unexpected trials to distinguish true prediction from neuronal adaptation to repeated stimuli. This can be achieved through control cascade stimuli in oddball paradigms [41,74], long inter-trial intervals to allow neuronal recovery [58], or by leveraging prior motor-sensory prediction experience (e.g., comparing mice trained on motor-sensory prediction versus motor-silent tasks) as elegantly done in isolating motor-sensory prediction in auditory cortex [69]. In parallel, it should be possible to monitor striatal dopamine signals; disrupting corticostriatal or dopaminergic pathways should spare SPEs but impact RP computations [64,65,75,76].

### Targeted learning versus continuous filtering

If the sensory cortex computes (or amplifies) RPs quickly and then cedes execution to subcortical circuits, necessity should be stage-dependent. During early acquisition, transient silencing of auditory cortex specifically during the outcome-prediction epoch has been shown to slow or prevent learning, with the same manipulation after criterion having limited impact on performance [27]. A simple test would be to change the task rules (e.g. new cue → reward delay or contingency reversal). In this case, the cortical network should re-engage, showing renewed reward prediction activity for a short period of time that is causal to new learning. By contrast, SPEs will vary their gain as statistics stabilize [22,74], as they rely on moment-to-moment comparisons within cortex.

### Domain generality: sensory, reward, and motor

The same L1-tuft/inhibitory gate should support three predictive readouts in sensory cortex:

- Sensory prediction: mismatch responses/SSA and laminar MMN-like activity reflecting local comparison of feed-forward input with contextual input to apical tufts [22,74,77].
- Reward prediction: reward-predictive signals that appear during discriminative instrumental learning and depend on long-range value-related inputs and neuromodulatory timing [25,27,43,63].
- Motor prediction: learned cancellation of self-generated sensory consequences and mismatch transients when action outcomes violate expectation as demonstrated in auditory cortex for self-generated sounds and in visual cortex for optic-flow predictions during locomotion/eye movements [68,70].

If the substrate is shared, tuft-targeting feedback or interneuron perturbations should degrade all three readouts within the same preparation, arguing for a domain-general predictive operation implemented on a common microcircuit.

### From specific mechanisms to general principles

The mechanistic proposal scales to a general principle: cortex predicts and compares where it can, and forwards predictions where comparison must occur elsewhere. This principle anticipates modality-invariant behavior (auditory, visual, somatosensory, olfactory), species-general signatures (laminar MMN in humans [77]), and task-invariant rules: when distal input carries sensory predictions, cortex computes SPEs; when distal input carries reward-related signals, cortex computes or amplifies RPs which are then used for downstream evaluation. The basal forebrain's activity in the superficial layers of auditory cortex (sound-locked plus state/value components [63]) exemplifies how a timed modulatory signal can align prediction with sensory evidence, an architecture that is likely reused across cortices. We see this section as a blueprint rather than an exhaustive catalog: the core prediction is that apical-tuft convergence and disinhibition are the common "gate," while content (sensory, value, motor) determines which computation is expressed.

### Caveats and alternative accounts

It is important to note that any future experiments should consider alternative possibilities. Not all deviance is prediction: SSA can reflect synaptic depression, so many standards and cascade controls, or long inter-trial intervals, remain essential to isolate SPE-like components [41,58,74]. Reward-timed activity may mix arousal, movement plans, and true reward prediction; rigorous state and movement measurements plus demixing analyses are needed [78,79]. Moreover, multiple routes deliver distal input to L1 including cortical (e.g. OFC), subcortical (e.g. amygdalo-cortical, higher-order thalamic), and neuromodulatory (e.g. cholinergic basal forebrain, noradrenergic locus coeruleus) and their weights likely vary with task, sensory modality and timescale [57,61,80]. Our claim is not a single privileged pathway, but a common circuit motif and rule of convergence.

In sum, the framework yields a compact set of falsifiable expectations: SPEs should be computable on a moment-to-moment basis and largely local; RPs should be most relevant during early learning and depend on downstream evaluation; both should rely on apical-tuft convergence gated by a local inhibitory microcircuit (of which disinhibition is one proposed mechanism). Showing these patterns in the same preparation—across sensory, reward, and motor regimes—would go a long way toward confirming (or refuting) the idea that a single cortical substrate implements a general predictive computation.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

This work was supported in part by NIH NRSA F31 (SJK), NIH R01 DC018650 (KVK), NSF CAREER (KVK), and NSF PHY-2309135 to the Kavli Institute for Theoretical Physics (KITP) (KVK).

## Data availability

No data was used for the research described in the article.

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This study shows that the auditory cortex is used for learning a sound-guided discriminative task but becomes dispensable once animals reach expert performance. The authors identify two higher-order computations in the auditory cortex that drive learning: (1) a fast-emerging reward prediction signal which is causal to learning, and (2) an action suppression signal that drives ongoing performance. Both signals are uncoupled from sensory representations, indicating a higher-order functional segregation within the auditory cortex that drives learning.

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