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An adaptive and flexible role for primary sensory cortex

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Classical views of sensory perception describe a hierarchical organization, extending from the sensory periphery to static representations in the primary sensory cortex, with downstream regions supporting decision-making and action. There is growing evidence that suggests a more flexible role of primary sensory cortex, with behaviorally relevant functions distributed across multiple levels of the early sensory pathway that can change in response to context. In this Perspective, we first examine primary sensory cortex beyond sensory representations through the lens of sufficiency to predict behavior. We then consider the necessity of primary sensory cortex in sensory-driven behaviors, explored through a range of inactivation and lesioning studies. Finally, we provide evidence that points to an adaptive and flexible role for primary sensory cortex, where function is shaped by experience and context. This adaptive nature demands a more holistic investigative approach that challenges sensory pathways with adaptive behaviors in response to changing environments, behavioral contexts and injury.

The adaptive nature of sensory signals

We live in a complicated world. Throughout our day, we navigate this complicated world through constant and continuous sensing of our environment. Peripheral sensors transduce touch on our skin, light entering our eyes and sound entering our ears, as well as odors entering through our nose and tastes coming into our mouth. All of these rich and dynamic signals are transmitted through independent pathways into the deep areas of our brain. The brain then extracts features from these inputs that are important for navigating our daily lives. The nature of this signaling has long challenged scientists and scholars, yet much remains unknown about even the most basic functions of these pathways. Ultimately, our senses support cognitive processes such as perception, decision-making and memory formation. It is tempting to view sensing and acting as separate processes; however, they are intimately associated, co-evolved and symbiotically acting in concert.

Early studies of sensing were focused on anatomical pathways originating from the peripheral sensors and involved tracing neural projections through nuclei and brain regions to establish the classical network of early sensory signaling that is still the bread and butter of neuroscience textbooks today. Physical stimuli such as photons of light, sound waves and vibrations on the skin are transduced into electrical signals that travel from the periphery through the specialized nerve fibers and through the thalamus to the primary sensory cortices—primary visual (V1), primary auditory (A1) and primary somatosensory (S1) cortices (Fig. 1a)—often with beautiful topographic organizations that are preserved, if not transformed, along the way[1–3] (Fig. 1b). Here we refer to the pathway from the periphery to primary sensory cortex as 'early', to distinguish these regions from higher-order regions along the hierarchy that are classically linked to decision-making and action. Although these brain regions are known to be recurrently connected anatomically, we as a community implicitly discuss signaling through the lens of a feedforward hierarchy that has evolved to extract increasingly complex and behaviorally relevant features at every stage along the way[4,5].

In this Perspective, we propose that early sensory circuits are more adaptable and flexible than traditionally recognized. We suggest that brain regions continually change their representations and relevance during learning, in response to environmental changes, or after injury, driven by parallel and reciprocal interactions (Fig. 1c). This process creates a 'moving target' within a highly distributed network, complicating efforts of researchers to attribute fixed functions to specific

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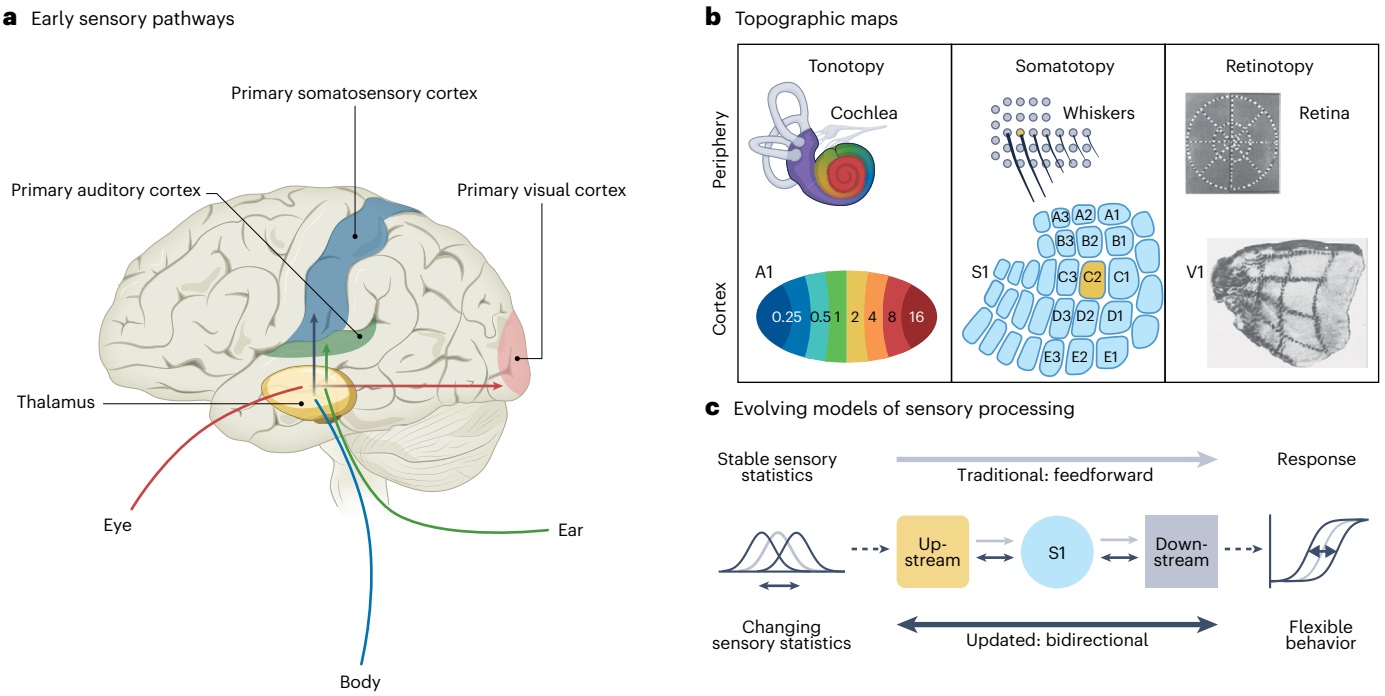

Fig. 1 | Basic principles of sensory processing from periphery to thalamus to cortex. a, Auditory, tactile and visual information is transmitted from peripheral receptors through the thalamus to primary sensory cortices (A1, S1 and V1), illustrating what is conventionally thought of as the 'early' feedforward stages of sensory processing. **b**, Sensory inputs from the periphery are topographically represented in primary sensory areas. Left, tonotopy in cat A1 cortex with different frequencies. Middle, somatotopic map in rodent S1 cortex with different whiskers. Right, retinotopic map in monkey V1 cortex with flickering bulls-eye pattern. Panel **b** is adapted with permission from ref. 1, AAAS and refs. 2,3, Elsevier (from right to left). **c**, Evolving views of how primary sensory cortex (S1) contributes to behavior. The signal flow at the top (gray; traditional: feedforward) shows S1 relaying input from stable sensory statistics to higher-order centers through unidirectional, bottom-up processing. The signal flow at the bottom (black; updated: bidirectional) reflects a flexible and distributed model in which S1 integrates changing sensory statistics with contextual signals from higher-order areas. Dashed arrows indicate general input–output flow. Single-headed arrows represent feedforward drive, whereas double-headed arrows denote bidirectional communication between S1 and both upstream (periphery, thalamus) and downstream (higher-order centers involved in decision-making) regions. This reflects a shift in thinking in the field—from viewing S1 as a passive relay of sensory input to recognizing its role in supporting adaptive behavior in changing environments.

brain regions. Recent findings provide evidence for this flexibility, showing that in scenarios with changing sensory statistics, the primary sensory cortex (S1) transitions from processing simple stimuli during basic detection to encoding signals necessary for adaptive behavior[6]. Specifically, as animals adapt to changes in sensory environments, S1 activity evolves to reflect behavioral strategies, rather than merely relying on sensory inputs. This context-dependent shift illustrates how the role of a brain region can change with experience, making it appear critical for a behavior in one study but not in another, depending on the task demands and stage of learning. Such flexibility might be the rule rather than the exception and has been overlooked by classical studies that did not sufficiently challenge the system. We hypothesize that this shift reflects a feedback process (that is, top-down influences) from higher-order cortical regions that reshape sensory cortical activity to integrate context-based and experience-based information. This, in turn, modulates subsequent feedforward signaling, aligning behavior with changing task demands. In this Perspective, we discuss growing evidence for the presence of signatures of behavioral signals in the early sensory pathway and the enigmatic role this pathway seems to have in behavior. Adaptive changes in behavior in response to a changing environment likely reflect an adaptive and flexible signaling scheme distributed across brain regions. While we focus on the tactile system, particularly the rodent whisker S1 (wS1), the concepts discussed apply broadly across sensory modalities.

The sufficiency of primary sensory cortex in behavior

We make thousands of decisions each day, most of them simple and small[7]. When studied scientifically in a reductionist manner, the textbook view of perceptual decision-making is that it involves gathering, combining and transforming sensory information into a behavioral response[8]. This is a particularly important process, as it bridges the divide from sensing to acting, along the sensorimotor arc. To better understand the neural pathways underlying these behaviors, laboratory animals can be trained to perform a specific sensory-guided behavior that involves decision-guided actions, while correlated neural signals from specific brain regions are measured over time. This approach has enabled the relatively direct assessment of the transformation from neural signaling to behavior[9]. In this way, a brain region would be considered 'sufficient' for the behavior if its neural activity predicts a behavioral outcome. Recent studies combining these behavioral paradigms with advanced neural recording techniques have challenged hierarchical models of sensory processing, suggesting that primary sensory areas may have a more flexible and integrative role than previously thought.

Sensory-behavioral transformation. Sensory detection is a great example that illustrates primary sensory cortex sufficiency (Fig. 2)—animals are trained in simple behavioral tasks, such as pressing a button or licking on a spout, in response to sensory stimuli. This is considered a 'simple task' because it involves presenting a single stimulus per trial and immediately generating a behavioral response. Such tasks require minimal perceptual, cognitive and motor integration, and typically involve relatively short training times. The correlated primary sensory neural signals are measured concurrently during task execution. The behavioral responses are categorized to calculate task performance based on the elements of signal detection theory[10]. Specifically, in a

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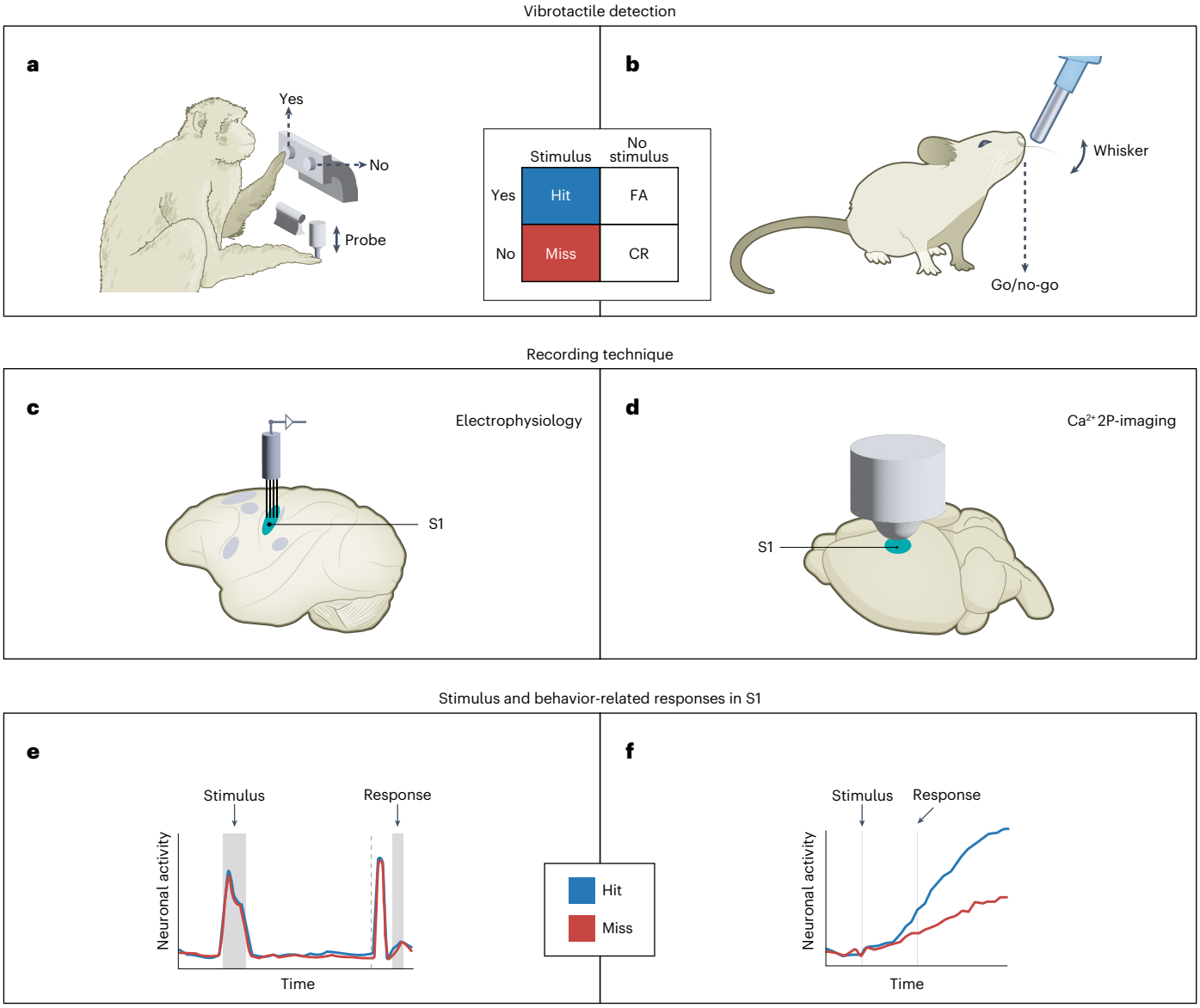

Fig. 2 | Neural representation of stimulus and behavioral responses studied with two distinct approaches. a, Tactile detection task in the monkey. Vibrations were delivered to the fingertip, and behavioral response was performed by pressing one of two buttons (yes/no). **b**, Tactile detection task in the mouse based on the deflections of a single whisker. The behavioral response is performed by licks on a water spout (go/no-go). Four trial types can be classified on the basis of the stimulus being present or absent and the behavioral response (yes or no); hit, miss, correct rejection or false alarm. **c**, Single-unit electrophysiology in the behaving monkey. Recorded cortical areas include S1 cortex (teal) and other areas (gray). **d**, Two-photon calcium imaging in mouse S1 (axons projecting from S2 to S1). **e**, Normalized neuronal population activity during hits (blue) and misses (red) for near-threshold stimuli in the behaving monkey. Dashed line indicates retraction of probe, gray rectangles indicate stimulus delivery and behavioral response. In this experiment, S1 activity does not appear to differ across outcomes, suggesting a lack of decision-related modulation. **f**, Mean $\Delta F/F_0$ activity in S1 axons from S2 during hit (blue) and miss (red) trials in the behaving mouse (two-photon Ca^{2+} imaging). Outcome-dependent differences in S1 responses suggest decision-related feedback from S2. Differences in technique and species contribute to differences in signal properties across panels. Panels **a** and **c** are adapted with permission from ref. 19, Elsevier; panel **e** is adapted from ref. 18, Springer Nature Limited; and panel **f** is adapted from ref. 39, Springer Nature Limited. CR, correct rejection; FA, false alarm.

stimulus trial, a 'hit' occurs when the participant responds correctly, typically leading to a reward, whereas a 'miss' occurs when the participant fails to respond to a stimulus in the manner required for a reward. During 'catch' trials, which occur in the absence of a stimulus, a 'false alarm' is recorded if the participant responds, whereas a 'correct rejection' is noted if there is no response. To ensure that the animal does not develop a bias or timed response, stimulus and catch trials are often drawn randomly with variable intertrial intervals. There is certainly a strong evolutionary pressure for animals to develop sensory detection skills that enable them to respond appropriately to their natural environment. Detection, with its simplicity and reactivity, serves as a foundational cornerstone for more intricate sensory processing—and it also provides clear evidence for primary sensory cortex sufficiency, as neural activity in S1 reliably predicts behavioral outcomes.

Sensory discrimination involves distinguishing between different sensory stimuli and is inherently more complex than detection. This complexity arises from the need to process multiple stimuli, often presented under varying temporal conditions—such as simultaneously, sequentially or with a delay requiring the storage and retrieval of sensory information—and, based on the comparisons, to generate the correct behavioral choice to receive a reward. These tasks demand greater perceptual, cognitive and motor integration,

and typically require longer training times. The term 'choice' is often used to describe behavioral decisions in these tasks, but its use depends on the context. In detection or discrimination tasks with multiple response options (for example, yes/no or forced choice), 'choice' accurately reflects the decision-making process. However, in paradigms with only one response option, such as go/no-go detection, the term can be misleading. For example, in no-go trials, it is difficult to determine whether the lack of an action reflects an active decision to withhold, or just simple distraction. In such cases, we refer to 'behavior-related activity' to more broadly describe neural and behavioral outcomes.

Behavioral neurophysiology was advanced through single-unit electrophysiology experiments in behaving primates (1980s and 1990s); detection or discrimination behavior was observed in parallel with electrophysiological recordings of sensory neurons[11–16]. A classic example is the comprehensive work discussed in refs. 17–19 that showed the mechanisms underlying tactile perception by training monkeys to detect or discriminate vibrations delivered to their fingertip (Fig. 2a). Electrophysiological recordings were classically limited to small neural populations within a single brain area at a time, but aggregated across experiments to explore numerous brain regions associated with sensorimotor behavior (Fig. 2c).

Using these approaches, the conventional perspective has been that primary cortical sensory areas extract information about stimuli in a somewhat static and representational manner[20], whereas secondary sensory cortex and higher cortical areas use this information to generate decisions[21,22]. By systematically measuring activity in many brain areas, these studies confirmed the amplification of choice-related signals along the feedforward pathway, supporting the classic hierarchical idea in sensory processing dynamics.

Expansions to the canonical feedforward model. More recently, sophisticated behavioral assays and psychophysical methods, adopted from human and primate work, have provided insight into the perceptual decision-making capabilities of rodent participants[23] (Fig. 2b)—mice and rats can efficiently integrate multisensory information[24,25], accumulate evidence over time[26,27] and adjust their behavioral strategies to optimize reward[28–31]. Recent technological advances within transgenic rodent models, such as optogenetics[32], two-photon microscopy[33] (Fig. 2d), wide-field fluorescence imaging[34,35] and large-scale electrophysiology[36], allow researchers to identify and manipulate single neurons and specific neuronal cell types. These techniques also enable measurements across larger areas, ranging from cell populations to brain regions. Imaging is less invasive than electrophysiology and amenable to long-term measurements; specific tissue volumes in the same animal can be repetitively imaged over the course of days, weeks or even months[37,38]. As increasingly improved data acquisition methods have become available in rodent models, researchers have increasingly challenged the canonical feedforward paradigm of perceptual decision-making, suggesting that this process may involve more complex and interactive neural circuits than previously thought. One example that illustrates both species and methodological differences comes from vibrotactile detection tasks studied using single-unit electrophysiology in primates[17,18] and multiphoton Ca^{2+} imaging in rodents[39] (Fig. 2). Both approaches use trained animals performing very similar reward-based detection tasks in which a stimulus may be present or absent, requiring an appropriate behavioral response that leads to the trial outcomes previously described. However, these studies reveal a divergence in the role of S1 in decision-making—in primates, single-unit recordings show no correlation between S1 activity and behavioral outcomes (Fig. 2e), whereas in rodents, S1 activity measured through multiphoton imaging is clearly correlated with behavioral outcomes, with decision-related signals attributed to feedback modulation from the secondary somatosensory cortex (S2; Fig. 2f).

Variable criteria for decision-related signals. The disparity in how decision-related signals are reflected in primary sensory cortex between primates and rodents may have several causes. One possibility is species differences, implying that primary sensory cortex in rodents differs from the canonical view in primates, both in function and in its role within the larger cortical network, where the rodent primary cortex may both extract sensory information and directly influence decision-making. Another explanation is that rodent methodologies provide greater granularity, more detailed data and statistical power, suggesting that experimental limitations in the primate studies might potentially have led to misinterpretations of the data. Finally, it is possible that the distinct behavioral paradigms used in rodent studies compared with primate studies challenge the system in a different way and capture only a snapshot of the flexible nature by which the brain deals with the challenge. It is important to note, however, that interpreting decision-related activity in primary sensory cortex is particularly challenging, as response behaviors like licking, whisking or lever pressing—as well as other uninstructed movements—can affect neuronal activity, confounding true decision signals[40]. In addition, the challenge of interpreting choice in certain paradigms, as previously discussed, further complicates this process. Careful controls—including delay periods, movement tracking and separation of task-related and movement-related variables—have enabled more robust experiments and analyses, providing strong evidence that primary sensory cortex integrates behavioral context, extending its role beyond basic stimulus processing.

Interestingly, human electroencephalography studies show response differences in primary sensory areas between correct and incorrect trials[41], suggesting that human and rodent data align more closely, with nonhuman primate data as the potential outlier. The presence of decision-related activity within S1 supports the notion that early sensory pathways possess the flexibility to integrate behavioral context beyond the basic processing of stimuli. Box 1 highlights decision-related activity in V1 and A1, complementing our focus on S1 and demonstrating that neural activity of other early sensory pathways also correlates with behavioral responses.

The necessity of primary sensory cortex in behavior

To explore the causal role of the primary sensory cortex in fundamental sensory behaviors, the researchers have traditionally disrupted its function by acutely silencing neuronal excitation, or chronically lesioning the region (Fig. 3). A brain region is considered 'necessary' for behavior if its inactivation disrupts the performance. A great example that illustrates primary sensory cortex necessity is the acute inactivation of excitatory S1 neurons in the rodent whisker system using optogenetic or pharmacological silencing. This acute manipulation results in impaired whisker detection performance[39,42–47]. In addition, optogenetic stimulation of excitatory S1 neurons can mimic whisker deflection during learning or task execution[43]. These findings underscore the causal role of S1 activity in supporting normal detection performance.

In contrast to acute inactivation, lesion studies suggest a more nuanced view on S1's necessity. The details in ref. 45 showed that complete ablation of S1 transiently disrupted detection performance; however, behavior typically recovered by the next session (Fig. 3a). Naive S1-lesioned animals could also learn whisker detection tasks, indicating the presence of compensatory mechanisms. Our results corroborate these findings[6]—ibotenic acid-induced lesions in S1 abolished neuronal signaling (measured with a genetically encoded voltage indicator) and impaired performance for one session, but task performance returned to baseline in subsequent sessions (Fig. 3a). This cumulative evidence suggests that, although S1 is the primary region for processing whisker-deflection signals, additional circuits can adapt to support stimulus–action–reward associations in S1-lesioned animals, reflecting mechanisms that may be at play in injury or disease.

BOX 1

Functional flexibility of V1 and A1 cortices

Studies in the visual and auditory pathways demonstrate that functional flexibility is a general principle of early sensory cortices, not limited to the somatosensory system. Below are relevant examples from these pathways that illustrate the functional flexibility.

Visual cortex (V1)

Decision-making. Beyond processing visual stimuli, V1 neurons are involved in decision-making during detection and discrimination tasks, with behavior-related activity linked to its columnar architecture[87,88]. Learning strengthens both anticipatory and behavior-related signals, thereby enhancing top-down processing during visual tasks[71,73].

Test loss of function. Transient optogenetic suppression of V1 severely impairs the ability to discriminate oriented gratings. However, permanent V1 lesions or injuries show mixed outcomes—some studies report a decrease in task performance[89], whereas others suggest compensatory mechanisms involving the superior colliculus or continued thalamic lateral geniculate nucleus input to extrastriate cortex, enabling relearning and partial recovery of function[90].

Auditory cortex (A1)

Decision-making. A1 neurons encode sound identity, choice-related signals and reward expectations during auditory discrimination tasks[91]. Neuronal activity in A1 predicts individual differences in fear learning, and neurons demonstrate learning-dependent selectivity for sensory inputs and rewards, which may facilitate associative memory formation[70,92].

Test loss of function. Transient optogenetic suppression of A1 impairs frequency discrimination, whereas permanent lesions have no impact on this ability, suggesting that alternative pathways rapidly compensate when A1 is permanently damaged[93].

This raises the question of which neural circuits compensate for S1 loss of function in the detection task. When intact, S1 likely supports detection by signaling to other cortical[44,46,48] and subcortical regions such as the higher-order thalamus (POm)[49,50], striatum[50–52] and superior colliculus[50]. These regions contribute to sensory-motor transformations and may adapt to compensate for the loss of S1. For example, descending outputs from S1 to these subcortical targets are critical for tactile detection[50], suggesting that they may take on compensatory roles. In addition, S2 may support detection through an alternative thalamocortical input from POm. The details in ref. 53 showed that POm can drive S2 activity even when S1 is disconnected, supporting the existence of an alternative route that may compensate for S1 loss. Such an alternative pathway could underlie the rapid behavioral recovery observed after S1 lesions[6,45] (see also Fig. 5c for a conceptual summary). Together, these mechanisms highlight the flexibility of the sensorimotor network and suggest that multiple pathways may support recovery of stimulus detection after S1 lesions. Similar compensatory systems likely also exist in other sensory modalities (Box 1).

However, this flexibility has limits. As task demands shift from simple detection to more complex sensory discrimination, the primary sensory cortex becomes indispensable. Discrimination tasks, like differentiating shapes[54] or textures[55,56], rely heavily on S1 owing to the increased cognitive, perceptual and motor coordination required. After S1 lesion or chemogenetic silencing, these tasks cannot be performed or learned, highlighting the crucial role of S1 in complex behaviors (Fig. 3b). Furthermore, S1's role becomes critical when context—such as variations in stimulus or reward characteristics—requires behavioral adaptation, even in tasks of consistent complexity[6]. For example, shifting sensory input statistics (random whisker-deflection amplitudes) revealed an adaptive strategy in mice that maintained reward accumulation. Chronic S1 lesions disrupted this adaptation (Fig. 3c), indicating S1's importance in experience-dependent sensory adaptation. This suggests that S1 has a key role in enabling animals to flexibly respond to changing environments—an ability essential for survival strategies.

These findings collectively indicate that S1 is essential for whisker-based detection behavior under normal conditions, while the recovery of function following S1 ablation underscores functional redundancy within the sensory pathway. Compensatory mechanisms allow other circuits to support basic detection tasks when S1 is disrupted. However, as task complexity increases or contextual demands shift, these compensatory pathways become insufficient. In such cases, S1 takes on a more critical role by integrating sensory inputs with contextual information, enabling animals to adapt flexibly to evolving demands.

Experience-dependent adaptive signaling in changing sensory environments

The nervous system is remarkable for its amazing ability to adapt to changes in the world, where the nature of the sensory environment shapes not only the fundamental sensory signaling[57], but also the behavioral strategies used to operate in a dynamic environment, which develop with experience over weeks and months. An experimental example of this behavioral adaptation is reversal learning—a discrimination task in which two different stimuli are associated with two different actions. Each specific stimulus is associated with a certain action. In the 'reversal task', the animal is charged with switching actions in response to the stimuli. In such complex tasks, where memory and heightened awareness go beyond simple detection's reactive nature, the cortex likely has a more crucial role. This supports the idea that the cortex, believed to enhance consciousness in associations[58], aids mental manipulation and cognition, enabling the learning participant to consciously grasp the 'rules of the game'.

Notably, studies that measure primary sensory cortex during behavioral adaptation observe that it is modulated in a correlative manner, reflecting the behavioral adaptation. For example, the details in ref. 56 showed the involvement of S1 in tactile reversal learning tasks (Fig. 4a). Mice were trained to discriminate textures with their whiskers. A 'rule switch' was then implemented by reversing the stimulus and reward contingency. Interestingly, S1 responses to the rewarded texture emerged during initial task learning, decreased after the rule switch and were then remapped to the newly rewarded texture (observed with two-photon Ca^{2+} imaging). The authors identified direct long-range feedback projections from the lateral orbitofrontal cortex (OFC) to S1 as responsible for this effect, motivated by the idea that OFC conveys task context and expected outcomes that could influence sensory processing in S1 (Fig. 4b). Thus, S1 chemogenetic silencing prevented learning of the basic task, while chemogenetic silencing of the OFC during the rule switch abolished both reversal learning and the corresponding S1 signaling.

Building on insights from inactivation studies and reversal learning, our investigation into the adaptive nature of S1 within the mouse vibrissa system provides an additional depth[6]. By imaging S1 with a genetically encoded voltage indicator, we found that S1 signals shifted from representing stimulus properties to transducing adaptive signals. In daily sessions, we measured S1 activity during basic

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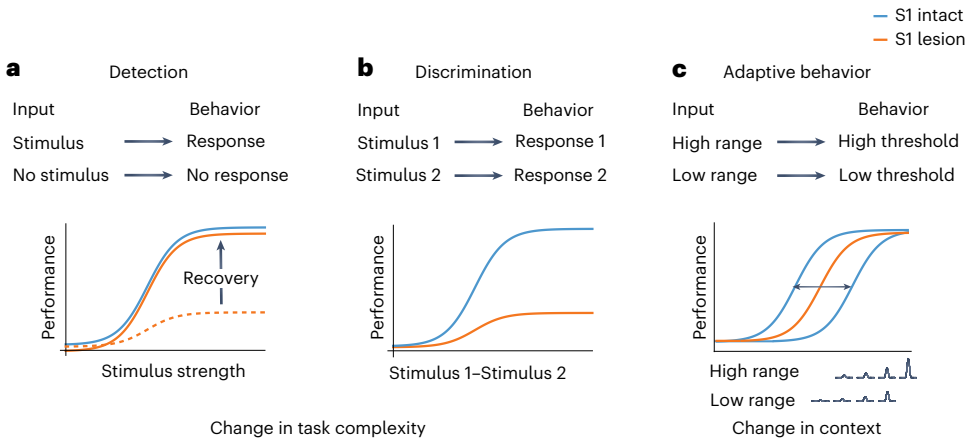

Fig. 3 | Evaluating behavioral performance in S1-lesioned mice. Effect of permanent S1 lesions on behavioral performance. Across all panels, blue psychometric curves represent performance in animals with S1 intact, whereas orange curves represent performance in lesioned animals. **a**, In detection tasks, the participant communicates the presence or absence of a sensory stimulus (for example, a whisker deflection) through licking a water spout. Psychometric curves show a transient deficit in detection performance in lesioned animals (dashed orange curve), followed by recovery after one session (solid orange curve). This suggests that although S1 normally supports stimulus detection, other circuits can compensate rapidly, enabling recovery[6,45]. **b**, In more complex discrimination tasks, the participant differentiates between various stimuli (for example, shapes or textures) and responds by licking specific water spouts corresponding to distinct stimuli (stimulus 1 or stimulus 2). Lesioned animals show degraded discrimination performance (orange), indicating that S1 is essential for executing complex sensory discriminations that impose greater perceptual and cognitive demands[54]. **c**, Adaptive behavior is evaluated by altering the stimulus context, such as shifting the range of presented stimuli (for example, high range versus low range), without altering task complexity. Animals with S1 intact adjust their response thresholds, reflected by a shift in psychometric curves (blue), to maintain reward accumulation across contexts. By contrast, lesioned animals show no shift in psychometric curves (orange), indicating that S1 is required for behavioral adaptation to changes in sensory context[6]. Panels **a** and **c** are adapted from ref. 6, CC BY 4.0.

detection learning, revealing that S1 sensitivity was driven by repetitive stimuli and unrelated to gradual behavioral changes. However, S1 activity increasingly correlated with behavioral adaptation after a prolonged exposure to changing context. As mentioned, head-fixed mice detected tactile stimuli of varying amplitudes, adapting their behavior to alternate between distributions of high and low amplitude whisker deflections (Fig. 4c). The sensory response in S1 was present from the start but gradually evolved with training experience to become context-dependent and adaptive, with the number of switches and sessions having key roles in this modulation (Fig. 4d). Notably, this effect is distinct from the adaptation properties of the neural circuits themselves[59], and only becomes apparent when consistently probed over extended periods, underscoring the need for longitudinal measurements.

Together, these findings illustrate how experience can shape sensory representations in primary cortex in a context-dependent manner, highlighting the need to consider top-down influences from multiple brain regions and distributed processing in models of sensory function.

Recurrent connectivity and distributed processing

The studies described here, along with many others, suggest a flexible role for these 'early' stages of sensory signaling, where certain functions are distributed across the sensory pathway rather than confined to specific areas. Despite the textbook description of sensing as a feedforward, sequential cascade, the modern established view is that sensory pathways operate bidirectionally, with each feedforward connection being matched by feedback or reentrant connections going from higher-order to lower-order cortical areas[60,61]. In feedback processing, higher-level representations provide contextual information to lower levels, facilitating perceptual functions and the formation of decisions[62]. Learning theories propose an experience-dependent shift in the balance between feedforward (or bottom-up) sensory drive and feedback (or top-down) modulation[63–68]. According to these theories, sensory processing is dominated by the bottom-up pathway in the naive condition, whereas learning and experience can enhance top-down modulation by higher cortical areas.

Predictive coding offers a specific mechanism that helps explain how and why this shift occurs[69]. In this model, cortical regions generate predictions about incoming stimuli and then compare these predictions to actual sensory input to identify mismatches, also known as 'prediction errors'. These prediction errors are propagated forward, allowing higher cortical areas to refine their predictions, thereby influencing how sensory information is processed at lower levels. As learning progresses, these top-down predictions become more precise, reducing reliance on bottom-up sensory input and minimizing prediction errors. This refinement represents a more efficient processing strategy, where sensory cortices prioritize expected stimuli, enabling more streamlined perception. In cases of disruption, such as lesions, compensatory pathways may sustain basic detection tasks by providing alternative signals. However, as tasks increase in complexity or contexts shift, the mismatch between sensory input and top-down predictions could become critical. Under these conditions, primary sensory regions are likely essential for processing prediction errors, enabling adaptive behavior and supporting efficient sensory processing.

Empirical evidence for this model demonstrates that reward-based learning in response to prolonged stimulus exposure can modify stimulus selectivity and behavior-related representations in the auditory[70], visual[71] and somatosensory[55,72] cortices. In mouse V1, sensory bottom-up drive (layer 4 excitatory neurons) gradually decreases, while top-down inputs from the retrosplenial cortex are enhanced during visual avoidance tasks over several days[73]. Experience-dependent transformations in cortical networks have also been reported on a global scale in humans. Extensive training on visual search tasks can reduce activity in the frontoparietal attentional network while shifting the cortical representation of the learned stimulus from higher to lower primary cortical areas, as measured by fMRI[74–77]. Along the same lines, although speculative, the emergence of the adaptive behavioral signals in S1 with experience (Fig. 4d) likely arises from top-down input from S2 to S1.

Notably, the distributed processing we describe here may even extend to earlier stages in the sensory signaling pathway. Our past research, using a detection of change paradigm, revealed cognitive signals in subcortical stages, illustrating decision-related signaling

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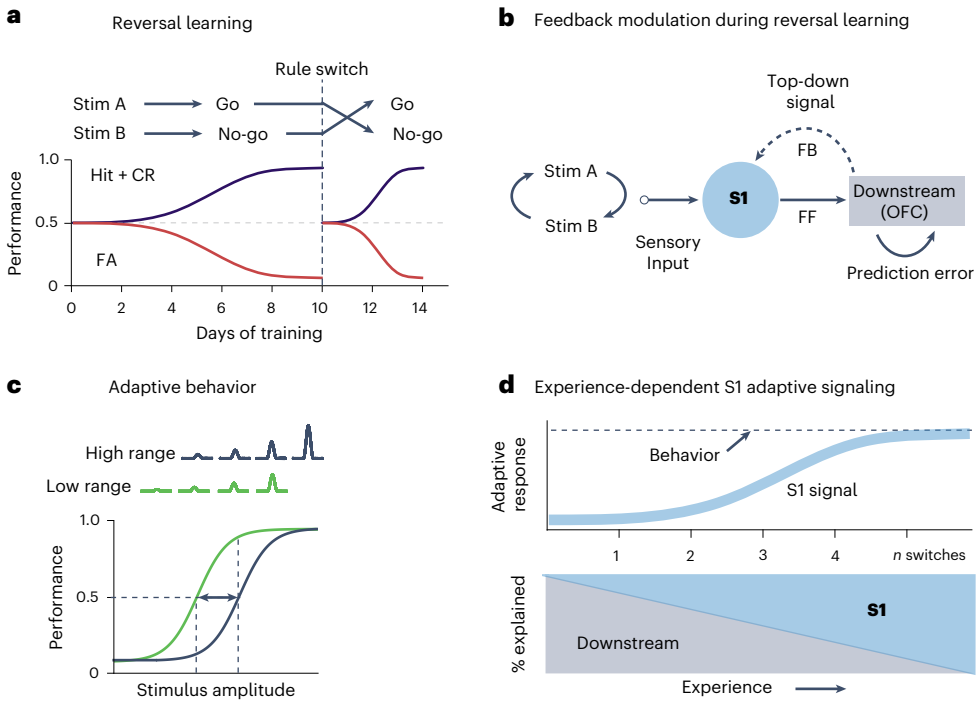

Fig. 4 | Adaptive sensing and decision-making. a, Reversal learning example. Mice were trained in whisker-based texture discrimination, followed by a 'rule switch' reversing stimulus and reward contingencies. Task performance was measured as mean correct rate (Hit + CR, purple) and FA rate (red). **b**, Schematic of feedback modulation during reversal learning. During reversal learning, feedback from downstream regions, such as the OFC, modulates activity in the primary sensory cortex (S1) based on the task context and expected outcomes. This feedback enables S1 to remap its sensory representations after a rule switch. In the case of OFC, such modulation supports value-prediction error computations that guide adaptive behavior. FB, feedback; FF, feedforward. **c**, Adaptive behavior example. Mice were trained to detect single whisker deflections with changes in stimulus statistics. Top, random amplitude whisker deflections were presented, with changes in the statistical distribution of the stimulus. The design includes amplitudes common to both high (dark teal) and low (green) range contexts. Bottom, psychometric curves represent adaptive behavior, illustrating a shift in response threshold (dashed lines and arrow) that helps maintain reward accumulation across contexts. **d**, Experience-dependent S1 adaptive signaling—stimulus statistics alternated across blocks of sessions (1 to *n* switches). Top, behavioral performance and S1 activity are plotted as adaptive responses, representing context-dependent changes (high versus low range). These responses reflect bidirectional changes, where behavioral and neuronal responses increase or decrease depending on the context. The behavioral response consistently demonstrates adaptability (dashed line), while adaptive signaling in S1 emerges gradually with experience (blue curve). Bottom, schematic illustrating the explanatory power of S1 (that is, how strongly neural activity predicts behavioral performance). The relative contributions of S1 and downstream regions are shown across different stages of experience. Panels **a** and **b** are adapted from ref. 56, Springer Nature Limited; panel **c** is adapted from ref. 6, CC BY 4.0.

in the primary sensory thalamus (VPm) of expert rats[78], yet it remains unknown as to how experience influences this phenomenon. This discovery raises questions about the overall flexible nature of the entire pathway. Mounting evidence shows that cortico-thalamic projections from cortical layer 6 substantially affect thalamic excitability[79–85], challenging the traditional view of the primary sensory thalamus as merely a relay station and prompting a re-evaluation of sensory processing and integration throughout the nervous system.

Thus, learning modulates bidirectional processing in sensory pathways, challenging traditional feedforward models. The predictive coding framework supports our theory that experience-dependent processes modulate sensory cortex activity by integrating bottom-up and top-down interactions to align behavior with changing sensory requirements.

Where do we go from here?

In this Perspective, we propose that sensory systems are more adaptable than traditionally recognized, with functions such as sensory detection, learning and decision-making being flexibly reallocated across multiple levels of the sensory pathway. We provide several lines of evidence to support this hypothesis. (1) Primary sensory cortex activity can reflect behavioral decisions. (2) When the primary sensory cortex is intact, its activity supports detection, but other circuits can compensate when it is impaired. (3) When faced with changing sensory context, the primary sensory cortex evolves beyond simple stimulus representation to transducing adaptive and context-dependent signals. (4) Learning modulates bidirectional processing within sensory pathways. These principles are synthesized in the conceptual framework shown in Fig. 5, using the mouse whisker system as an illustrative model. The framework illustrates one possible pathway, however, other mechanisms may also contribute to the observed effects.

Once considered the center for basic sensory representations, the role of the primary sensory cortex is now increasingly understood to be flexible and context-dependent, shaping behaviors from basic stimulus detection to complex adaptive responses. This evolving function moves beyond traditional feedforward models, as demonstrated in studies investigating decision-making, learning, behavioral adaptation and loss-of-function perturbations.

To gain a deeper understanding of sensory processing, future research should adopt a holistic approach. Experimental frameworks need to prioritize measuring activity in detail across multiple brain structures, acknowledging the diverse mechanisms and timescales underlying sensory tasks. A shift from spatially confined representations to a more comprehensive understanding of the time-sensitive interactions between brain regions is essential. Using advanced technologies, long-term studies will be crucial in capturing the evolving functions of sensory pathways, particularly in the context of adaptive behaviors and learning. A key aspect of these experiments is controlling behavioral complexity by systematically manipulating task difficulty and context to challenge behavioral strategies. The adaptive behavior described

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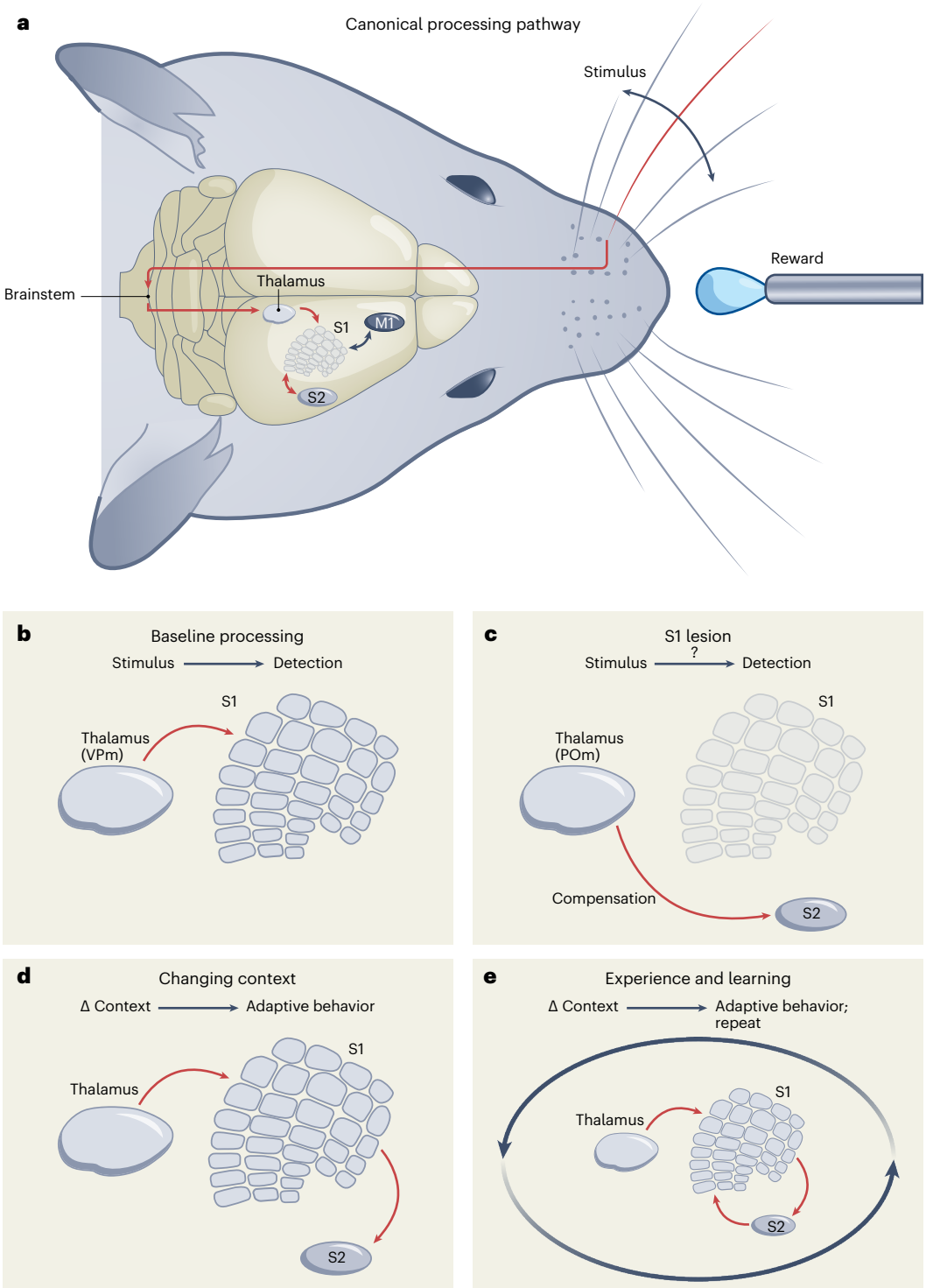

Fig. 5 | Possible adaptive roles of S1 across behavioral conditions. a, Canonical pathway in the mouse vibrissa system. Whisker deflections activate trigeminal sensory neurons, which synapse in the brainstem. Signals are relayed through the ventroposteromedial nucleus of the thalamus (VPm) to S1, where sensory information is processed and transmitted to downstream areas (for example, S2 cortex) for decision-making and to M1 to guide a behavioral response. Successful detection leads to reward. Panel **a** is adapted with permission from ref. 2, Elsevier. **b**, Baseline processing. In stable conditions, S1 receives VPm input and supports detection by conveying behaviorally relevant signals. **c**, S1 lesion. When S1 is removed, alternative pathways, such as input from the posterior medial nucleus of the thalamus (POm) to S2, may compensate to preserve detection behavior[45,53]. **d**, Changing context. During initial exposure, modulated activity in downstream areas (for example, S2) is thought to support adaptive, context-dependent behavior. **e**, Experience and learning. With repeated exposure, top-down input (for example, from S2) is proposed to engage S1, enabling the emergence of adaptive signals that support flexible behavior[6]. M1, motor cortex.

here reflects shifts in the strategies animals use to optimize or maximize rewards, seemingly constrained by the effort required to do so. Measures of reward signaling[86] are likely crucial for fully understanding the processes driving the adaptive nature of sensory pathways.

In summary, the path forward involves an extension from questions of 'where?' to questions of 'how?' and 'when?' as we explore the flexible nature of sensory signaling. By challenging the idea of attributing specific functions to certain brain regions, this Perspective opens

new possibilities for understanding neural circuits. Examining the parallel and reciprocal interactions within sensory pathways, along with their time-dependent, flexible roles in increasingly complex tasks and changing contexts, will help resolve conflicts across studies and reveal the neuronal processes underlying adaptive behavior.

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