Review

We Are Our Receptors: Rethinking Cortex and Cognition from The Sensory Periphery

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Review

We Are Our Receptors: Rethinking Cortex and Cognition from The Sensory Periphery

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Abstract

Current neuroscience situates cognition within cortical and (to a less extent) subcortical areas, relegating receptors to passive relays. We propose a receptor-centered framework in which receptors act as constitutive determinants of neural architecture and cognitive experience, supported by empirical studies that substantiate our interpretation. Opsin gene therapy altering color vision in adult primates, as well as cross-modal reorganization in congenital or acquired human blindness, show that natural or artificial modifications of receptor repertoires can reshape cortical maps and perception. Mechanoreceptors and proprioceptors can sustain the representational scaffolds for agency, motor planning and body schema, while the interoceptive receptors that detect respiratory, cardiovascular and visceral states can modulate affect, memory and perceptual awareness. Also, we propose that gut bacteria may contribute to cognition through receptor-mediated signaling, where microbial metabolites interact with neural, immune and endocrine receptors to influence mood, motivation and higher cognitive processes. We argue that receptor guidance may extend upward into cognition: mental imagery, sensory substitution and synesthesia point towards imagination and abstract thought as recombination of receptor-derived primitives. Comparative neurobiology reinforces our claims, showing that distinct receptor repertoires yield species-specific perceptual worlds such as echolocation in bats, polarization vision in cephalopods or magnetoreception in birds, each shaping unique cognitive landscapes. Overall, cognition could be described as a multilevel process in which cortical activity is driven by receptor-encoded informational templates that are established across phylogeny, ontogeny and individual experience. To think is to reconfigure receptor traces, while to imagine differently is to sense differently.

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Introduction

For much of modern neuroscience, the cerebral cortex has been regarded as the primary locus of cognition. From early phrenological attempts at mapping faculties, through Broca's and Wernicke's clinico-anatomical correlations, to contemporary functional imaging studies, cognitive processes have been consistently localized to cortical networks (Weisberg et al., 2024; Zhang et al., 2023). More recently, cognitive capabilities and higher-order processes have been attributed to subcortical regions as well (Crosson 2021; Janacsek et al., 2022), with strong evidence emerging for the striatum (Chuhma et al., 2023; Castro et al., 2024) and the cerebellum (Schmahmann 2019; Jacobi et al., 2021; Rudolph et al., 2023). Within this framework, sensory receptors are usually cast as passive transducers, channels delivering information to the "real" cognitive machinery.

This view, however, overlooks that receptors are not passive relays of information but may stand as determinants of the cognitive architectures elaborated by cortical circuits (Fritzsch et al., 2019; Mancuso et al., 2009). We argue here that neural dynamics cannot be disentangled from the receptor repertoires sculpting them: photoreceptors establish visual categories, mechanoreceptors define tactile representations, chemosensory and interoceptive receptors shape affective and bodily states,

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etc. (Grabska-Barwinska et al., 2017; Fettiplace 2023; Willoughby et al., 2021). Cortical and subcortical dynamics remain central to cognition, yet they can be better understood as plastic maps inscribed by receptor repertoires.

Our review advances a receptor-centered approach in various steps (see Table 1 for a roadmap). First, we assess evidence that receptors shape cortical maps, including plasticity induced by adult interventions like gene therapy. Also, we examine blindness and sensory deprivation as natural experiments in cortical reorganization. Second, we consider touch and proprioception as receptor systems grounding agency and body schema. Third, we analyze interoceptive receptors as contributors to affect, memory and consciousness. Fourth, we propose that thought and imagination are recombinations of receptor-derived primitives and explore the speculative possibility of hidden receptor systems. Fifth, we extend the model to comparative biology, where receptor repertoires generate species-specific *Umwelten*. Finally, we integrate these strands into a receptor-centered framework for neuroscience, while also addressing its limitations, outlining future directions and considering broader implications for cognition and brain theory.

Table 1. Core steps of a receptor-centered approach. The table summarizes the key steps developed throughout our review, culminating in an integrated receptor-centered framework for cognition.

Step	Explanation / Evidence
Receptors repertoires inscribe cortical maps	Adult plasticity is shown by gene therapy restoring color vision in primates, while both congenital and acquired blindness reveals cortical flexibility grounded in receptor absence or substitution.
Touch and proprioception	Mechanoreceptors and proprioceptors provide representational scaffolds for body schema, agency and motor cognition, with proprioceptive loss reorganizing motor strategies.
Interoception	Baroreceptors, chemosensors and visceral receptors shape affect, memory and the conscious experience of bodily states; receptor dysfunction alters emotional regulation and self-awareness.
Imagination, thought and theoretical hidden receptors	Imagination and thought recombine receptor-derived primitives, as shown by mental imagery, sensory substitution and synesthesia, while possible hidden systems suggest that cognition is receptor-bound.
Species-specific Umwelten	Divergent receptor repertoires generate distinct perceptual worlds (e.g., bat echolocation, mantis shrimp vision, mosquito chemosensitivity) highlighting cognition as receptor-relative.

Chapter 2. Receptors as Architects of Cortical Maps

The cerebral cortex has traditionally been interpreted as a reflection of intrinsic computational principles, from early column theories to modern connectomics. Recent work highlights the distributed cortical dynamics underlying cognition in action (Xie et al., 2023; Grossman et al., 2023), characterized by hierarchical organization, recurrent connectivity and multimodal integration (Weisberg et al., 2024). Circuit-level studies emphasize the interplay of neurons, synapses and glia (Yuste et al., 2020), while multiscale maps reveal how synaptic motifs and fiber tracts sustain function (Zhang et al., 2023). Collectively, the cortex, and to a less extent the subcortical structures, stand for a dynamic, adaptive network capable of generating complex mental states from its internal architecture.

Yet mounting evidence shows that this cortical machinery is not autonomous, but rather is sculpted by the very receptors channeling environmental signals. Altering receptor repertoires reshapes cortical territories and, in some cases, expands perceptual experience itself. Landmark experiments introducing the human long-wavelength opsin into dichromatic monkeys endowed them with trichromatic vision, revealing that cortical maps reorganize to integrate novel receptor inputs even in adulthood (Mancuso et al., 2009). Comparable evidence arises in olfaction, where receptor diversity and density shape both detection and the geometry of cortical odor maps (Grabska-Barwinska et al., 2017) and in audition, where cochlear receptor distributions determine cortical tonotopy (Fettiplace 2023).

Flexibility is not a property of the cortex alone but reflects its capacity to continually remap according to the sensory roadmap provided by receptors. To modify receptors is to reconfigure the very coordinates of cognitive space. For instance, prenatal and neonatal odor cues guide feeding, bonding and survival from the earliest stages of life, showing how receptor systems scaffold not only adaptation, but also attachment and care (Shafaati Laleh et al., 2025). Conversely, alteration of receptor input can destabilize perception. A case of cerumen-induced hearing loss produced transient auditory hallucinations that resolved with receptor restoration, demonstrating how receptors could directly shape cognitive outcomes (Spiegel et al., 2012).

Overall, cortical maps are not abstract self-organizing patterns or autonomous wiring diagrams, but adaptive surfaces on which receptor repertoires inscribe the scripts of experience. Cortical networks provide the substrate, while receptors provide the categories of possible inputs making experience and cognition possible. In the next paragraph, blindness and sensory deprivation are examined as natural experiments in receptor-driven cortical reorganization.

Sensory loss and cortical reorganization. Receptors inscribe the first drafts of cortical organization, with brain circuitry adapting around receptor-generated maps. Evidence from developmental neurobiology supports this view: primary sensory maps are initially established through molecular guidance cues and activity-dependent refinement before central cortical circuits mature (Fritzsch et al. 2019). Each modality develops a distinct topography, shaped by receptor-specific signals and chemoaffinity rules, so that cortical architecture emerges in response to receptor-driven inputs rather than in isolation. Other studies reinforce this principle. Visual and somatosensory circuits segregate only under receptor-driven activity, emphasizing that sensory input is necessary for modality-specific mapping (Guillamón-Vivancos et al., 2022).

Blindness provides a striking natural experiment in receptor deprivation, revealing how cortical territories reorganize in the absence of visual input. It compels the question of what becomes of the cortex when its primary receptor inputs are absent from birth or lost later in life. The emerging answer is that the cortex does not preserve a fixed architecture, but rather reorganizes around available receptor signals, demonstrating its dependence on peripheral inputs.

Congenital blindness illustrates this principle most clearly. In the absence of retinal input, the occipital cortex is colonized by tactile and auditory functions. Braille reading recruits regions traditionally associated with vision, while auditory localization engages occipital territories with striking precision, demonstrating that cortical fields are not intrinsically visual but await inscription by receptors individuals (Haupt et al., 2023). Structural imaging confirms strengthened networks linking occipital and non-visual regions in the congenitally blind (Jiao et al., 2023). Thalamocortical rerouting studies further reveal rapid redirection of tactile information into visual pathways (Müller et al., 2019).

Acquired blindness, by contrast, produces partial reorganization but preserves vivid visual imagery. When receptor input is removed after development, cortical maps retain their sensory "imprint", enabling imagination even in the absence of ongoing input. This explains why motor imagery and learning of sound localization in blind individuals are modulated by prior visual experience (Imbiriba et al., 2006; Tao et al., 2017). Research on tactile spatial scaling shows that both early- and late-blind individuals adaptively scale tactile maps, but with greater reliance on proprioceptive strategies in the early blind (Szubielska et al., 2024). Still, reduced acuity in low vision likewise diminishes the clarity of mental images, suggesting once again that imagery fidelity depends on receptor integrity (Arditi et al., 2021).

Taken together, evidence from congenital and acquired blindness reveals that cognition is plastic because receptors write cortical maps. The absence of a receptor system is not simply a subtraction, but a reconfiguration of the cognitive field. Where receptors never spoke, cortex never acquired their language; where they once spoke, echoes remain.

This reframing extends beyond blindness. The restoration of thermal sensation in amputees, through a wearable interface that projects phantom temperature percepts onto residual skin, demonstrates how engineered receptor-like pathways can recreate embodied experience (Iberite et al., 2023). When designed according to receptor principles, namely, matching transduction, spatial mapping and feedback, theses artificial systems effectively reconstruct natural sensory inscription. In the next chapter, we turn to touch and proprioception, exploring how these receptor systems can scaffold agency, motor control and the sense of bodily self.

Chapter 3. Touch and Proprioception: From Body to Cognition

Touch has often been relegated behind vision and audition, yet its receptor landscape is among the most complex in the body, since the skin contains a rich repertoire of mechanoreceptors, each tuned to distinct aspects of pressure, vibration, texture and stretch (Severson et al. 2017; Neubarth et al. 2020; Emanuel et al. 2021; Ojeda-Alonso et al. 2024). Developmentally, touch is the earliest sensory modality to scaffold cortical organization in utero (Marx 2019). We argue that touch is not merely an interface for detecting objects but is constitutive of body ownership, agency, social bonding and symbolic cognition. Tactile receptor architectures are so accurate to capture spatial detail at the scale of fingerprint ridges, with stable receptive subfields persisting across scanning speeds and directions (Jarocka et al., 2021). These microstructures allow cortical texture and object recognition, demonstrating once again that cognitive richness originates in receptor-level encoding (Longo 2017). Pathological cases underscore the multitasking of somatosensory receptors: *Staphylococcus aureus* co-opts pruriceptive pathways by activating a V8 protease–PAR1 signaling axis, driving aberrant neuronal excitation, compulsive scratching, and subsequent tissue damage (Deng et al. 2023). This demonstrates that pathogen-mediated receptor manipulation can reprogram sensory coding, linking peripheral receptor activation to maladaptive behavioral and perceptual outcomes.

Sensorimotor crosstalk s between touch and posture. A relationship does exist between tactile and proprioceptive receptors, linking embodiment and agency from the very beginning of life. Neonates integrate tactile and proprioceptive cues within hours of birth to establish a primitive self-model (Della Longa et al. 2016). Perceptual signals may originate from receptor encoding dynamically modulated by body mechanics, as demonstrated by evidence that postural states influence tactile processing already at the receptor level, prior to cortical interpretation. The effects of proprioceptive modulation are evident also in the motor circuits of flies, where a single motor neuron produces directionally distinct movements as a function of head posture (Gorko et al., 2024), while receptor-driven synaptic architectures underlie the generation of visually guided escape behaviors (Dombrovski et al., 2023). Still, tactile processing in humans is posture- and location-dependent, with parietal areas decoding spatial configurations and somatosensory cortex tracking form-related changes (Ambron et al., 2024).

Evidence from development and learning underscores the constitutive role of tactile and proprioceptive receptors also in higher cognition. In preschoolers, strengthening object-control skills produced parallel gains in executive function, with dose–response links (Capio et al. 2024). Systems-level recordings show that even cortical areas for decision-making are pervaded by proprioceptive inputs (Stringer and Pachitariu 2024). Cross-modal interactions reinforce this account. Tactile and auditory signals converge early within hours of birth, shaping each other's cortical representations (Fang et al. 2017; Ronga et al. 2021; Zhou et al. 2021). Visual–tactile integration supports probabilistic inference, while vibration can recruit auditory midbrain pathways (Huey et al. 2024). Furthermore, social and affective touch relies on C-tactile afferents (Morrison and Olausson 2011), extending into memory and affective networks (Stoeckel et al. 2021).

Motor control and receptors. Motor control studies suggest that efficiency and flexibility emerge from receptor-driven loops. A "virtual rodent" model shows that reinforcement learning trained on biomechanical constraints can predict motor and striatal activity better than kinematics, suggesting receptor-informed inverse dynamics (Aldarondo et al. 2024). The spinal stretch reflex, mediated by proprioceptive pathways, can generate efficient postural corrections, embedding control laws in peripheral loops (Weiler et al. 2019). Proprioceptive receptors like muscle spindles, Golgi tendon organs and vestibular sensors ground motor control and the sense of agency. Indeed, their disruption can produce severe cognitive deficits, forcing patients to rely on vision for the simplest movements (McNeill et al. 2008). Zhao et al. (2025) show that the compound eye's structural organization in *Drosophila* determines the tuning of T4/T5 motion-sensitive neurons, shaping optic flow processing and locomotor control. This underscores the intimate link between receptor arrays, neural computation and motor behaviour, illustrating how sensory architectures can constrain motor strategies. Sheng et al. (2025) demonstrate that motor learning dynamically remodels cortico-striatal axonal boutons in the adult mouse brain. Boutons selective for rewarded movements were stabilized, whereas those linked to unrewarded actions were pruned. This bouton-level plasticity shows that motor skill acquisition may reorganize cortico-striatal outputs, integrating receptor-driven proprioceptive inputs with striatal remodeling to support the emergence and consolidation of new cognitive–motor strategies.

In mice, decision-making is distributed across cortex, basal ganglia, cerebellum and thalamus, with evidence integration tightly bound to peripheral movement states (Khilkevich et al. 2024). Furthermore, EEG studies show that variability in locomotor adaptation speed reflects spectral differences in parietal, sensorimotor and visual cortices, linking individual learning differences to receptor-modulated oscillations (Jacobsen and Ferris 2024). The looming-evoked avoidance reflex exemplifies how sensory architecture transforms perception into action. In both insects and vertebrates, specialized visual receptors detect approaching stimuli and trigger rapid escape responses through reflexive pathways that operate independently of cortical control (Chen et al., 2022; Calanni et al., 2024). This mechanism shows that receptor organization not only enables detection, but also defines the speed and structure of behavioral reactions, revealing cognition as rooted in receptor-level processing.

New perspectives extend receptor centrality to other organs. For instance, bones can function as sensory organs, since skeletal interoception transmits signals to the hypothalamus to orchestrate stem cell differentiation, osteoblast/osteoclast activity and repair (Xiao et al. 2023). Mutations reinforce the principle: PIEZO2 variants cause musculoskeletal disorders like arthrogryposis and are implicated in migraine (Della Pietra et al. 2020; Qin et al. 2021; Shin et al. 2021; Ma et al. 2023; Santiago et al. 2025).

Taken together, these findings converge on our hypothesis: touch and proprioception are not peripheral relays but constitutive cognitive systems. Their receptors inscribe cortical maps, shape motor control, scaffold selfhood, mediate immunity and repair, extending into symbolic and affective domains. In the next chapter, we turn inward to interoception, examining how visceral and metabolic receptors extend this model to affect, emotion and consciousness.

Chapter 4. Interoception, Taste and Olfaction

While exteroceptive and proprioceptive systems ground our relation to the external world and to the body's posture and movement, interoception refers to the perception of internal bodily states (Horsburgh et al. 2024; Feldman et al., 2024; Subramanian and Thaiss, 2024). It integrates signals from organs like the gut, heart and lungs, supporting awareness of conditions like hunger, thirst, heartbeat, visceral arousal, etc. Beyond conscious sensations, interoception conveys information about less visible dimensions of bodily function, including gut distension, immune signaling, thermoregulation and metabolic balance, thereby contributing to the neural regulation of physiological homeostasis. Long neglected in cognitive neuroscience, interoceptive receptors are now recognized as shaping emotion, motivation, decision-making, memory and even perceptual awareness.

Gut–brain interfaces, microbial signaling and nutrient coding. The gut–brain axis provides a paradigmatic case for receptor-centered cognition. Vagal and spinal afferents convey microbial and metabolic signals from the intestine to the brain, shaping mood, cognition and social behavior (Han et al., 2022; Siopi et al., 2023; Hwang and Oh, 2025). Some of these influences are explicitly receptor-mediated. For instance, microbial metabolites can regulate vagal activity and central processing via defined receptors (Jameson et al., 2025). In mice, the bacterial cell-wall sensor Nod2 is expressed in hypothalamic GABAergic neurons, where muropeptides suppress feeding and tune thermoregulation (Gabanyi et al., 2022). Direct neurobacterial interactions reinforce our claims. Live bacteria adhering to neurons alter calcium dynamics, synaptic proteins and neuroplasticity-linked transcription, underscoring receptor-based microbial modulation (Lombardo-Hernandez et al., 2025). Microbiome-derived endocannabinoids can drive dopamine release during exercise via TRPV1-positive sensory neurons (Dohnalová et al., 2022), while microglia-mediated circuit remodeling depends on the microbiota to sustain social behavior (Bruckner et al., 2022). A gut-produced metabolite, 4-EPS, alters oligodendrocyte function and myelination, leading to anxiety (Needham et al., 2022). Microbiota also constrains HPA-axis stress pathways through glucocorticoid receptor signaling (Wu et al., 2021).

At the population level, metagenomic studies reveal associations between depression and dopamine- and GABA-related microbial modules, highlighting receptor-mediated pathways through which gut chemistry can shape affective states (Valles-Colomer et al., 2019). Complementing these findings, human cohort studies in children link gut microbial taxa and microbial genes to cognition and neuroanatomy, suggesting that receptor-mediated microbial interfaces actively sculpt developmental trajectories (Bonham et al., 2023). Adding to this expanding picture, Liu et al. (2025) show that colonic neuropod cells can detect the microbial protein flagellin via Toll-like receptor 5, releasing peptide YY onto vagal neurons to regulate feeding. This receptor-based pathway demonstrates once again that behavior can be directly driven by microbial cues.

In the domain of nutrition, food itself exemplifies the receptor logic of interoception. The detection of dietary ω-6 linoleic acid through the FABP5–mTORC1 signaling cascade directly links macronutrient composition to neural plasticity and behavioral regulation (Koundouros et al., 2025). Moreover, nutrients in the small intestine engage distinct ensembles of enteric neurons via epithelial transduction pathways, such as serotonin-mediated signaling, rather than through direct neuronal contact (Fung et al., 2025). These findings suggest that the gut operates as a receptor-based coding system, translating chemical compositions into structured neuronal activity patterns that propagate through the enteric and central nervous systems. Accordingly, eating could be redefined not as a passive metabolic process, but as an active sensorimotor dialogue between environmental chemistry and neural computation, in which cognition extends into the visceral domain.

Overall, microbial ligands and nutrients can be transduced by immune, neural and endocrine receptors. These systems continuously write streams of bodily information into neural circuits, gating perception, biasing decisions, motivating behavior and scaffolding memory.

Respiration, cardiovascular sensing and visceral afferents. Respiratory and cardiovascular sensing, each equipped with specialized receptor systems, likewise demonstrates the extensive reach of interoception. It is well known that respiration-driven rhythms can shape emotional cognition and memory (Folschweiller and Sauer 2021). Reviews converge: breathing organizes cortical oscillations into predictive temporal gradients scaffolding perception and action (Brændholt et al., 2023), while inhalation–exhalation phases dynamically modulate neural excitability and attention (Heck et al., 2022). Nasal respiration enhances odor memory consolidation after encoding, whereas mouth breathing abolishes this benefit, directly implicating respiratory afferents in mnemonic stabilization (Arshamian et al., 2018). Intracranial recordings show inspiratory peaks that modulate fear discrimination and memory retrieval, while diverting airflow to the mouth weakens these effects (Zelano et al., 2016).

Heartbeat-locked baroreceptor activity biases visual awareness and decision thresholds, revealing that systolic and diastolic phases gate the timing and content of perceptual events (Park and Tallon-Baudry, 2014; Veerakumar et al., 2022). Time perception itself expands and contracts within each heartbeat, with arousal shifting the systole–diastole balance (Arslanova et al., 2023). Even at the cellular scale, heartbeat-related modulation of extracellular spikes helps classify human neuronal subtypes in vivo, tying interoceptive motion to electrophysiological identity and oscillatory coupling (Mosher et al., 2020). Together, cardiorespiratory signals emerge not as background noise but as rhythmic priors that entrain cortical timing, memory and affect.

Visceral afferents provide further evidence of receptor-level specificity. Brainstem circuits encode visceral sensations with high resolution, composing ascending interoceptive channels that deliver receptor-defined information to forebrain targets (Ran et al., 2022). In the urogenital system, the mechanosensitive channel PIEZO2 plays an indispensable role: expressed in the urothelium and sensory neurons, it enables bladder stretch detection and micturition reflexes. Loss of PIEZO2 in both mice and humans impairs filling sensation and coordination, situating a single receptor as the linchpin of urinary control (Marshall et al., 2020). These cases underscore how interoceptive receptors may convert mechanical and chemical states of the body into structured perceptual categories.

Taste and olfaction at the boundaries of interoception. Taste extends the specificity of interoceptive signaling, demonstrating how diverse receptor systems can transduce internal states into perceptual and cognitive phenomena. Oral cooling and warming, for example, are dissociable at the receptor level via TRPM8, which is indispensable for cold perception and for generating the qualia of thermal contrast (Li et al., 2024). The catalogue of basic tastes has expanded, since ammonium has been recognized as a sixth basic taste quality, detected by dedicated transduction mechanisms (Roper et al., 2019). Shimizu et al. (2025) used AlphaFold3 to predict the three-dimensional structures of 25 human bitter taste receptors, revealing variable extracellular domains crucial for ligand diversity expressed in oral and extraoral sites, including the gut–brain axis. These predictions underscore how receptor architecture might enable broad chemosensory coding, linking taste perception to systemic health, metabolism and cognition. Strikingly, mammalian taste cells express not only gustatory receptors but also functional olfactory receptors, revealing a surprising cross-modal chemosensory convergence within the mouth (Malik et al., 2019). These findings suggest that taste is not limited to discrete flavor categories, but operates as part of a multimodal receptor network integrating external chemistry with internal states.

Olfaction holds a distinctive position, transducing environmental chemistry into experiential states that are at once visceral, mnemonic and affective. Humans display roughly 400 olfactory receptor types, each broadly tuned, yielding a high-dimensional odor space that nonetheless supports reliable behavioral judgments across cultures (Keller and Vosshall, 2016). These receptors do not act in isolation but operate in concert, scaffolding and calibrating one another across modalities (Cai et al., 2024). Recent advances integrate chemistry with psychophysics to predict perceptual similarity and identification performance, offering data-driven maps of the odor landscape (Lee et al., 2023). Cross-cultural lexicons reveal shared odor categories, particularly for body odors, suggesting that receptor repertoires impose constraints on olfactory cognition and even on the structure of language (Bierling et al., 2025a; Bierling et al., 2025b). At the neuronal level, olfactory coding extends deeply into affective and cognitive circuits. Cross-modal responses to odor-related words and images reveal concept-like coding embedded in olfactory pathways (Kehl et al., 2024). In this sense, smell bridges biology, memory and meaning, exemplifying how receptor repertoires can shape not only perceptual experience, but also symbolic systems and cultural practices.

Taken together, taste, temperature and olfaction illustrate how receptors delineate the boundary zones between external and internal sensing. These modalities highlight that the very distinction between interoception and exteroception is porous: receptor repertoires continuously translate chemistry, pressure and thermal states into signals defining both subjective experience and shared human culture. Therefore, interoceptive receptors stand for the architects of the inner scene, generating the categories and rhythms from which affect, valuation and awareness are composed. In the next chapter, we turn to imagination and abstract reasoning, arguing that even our highest capacities could be understood as recombination of receptor-derived primitives.

Chapter 5. Thinking in Known and Unknown Receptors

Imagination and abstract thought are often portrayed as disembodied capacities detached from the sensory systems, taken to their logical extreme in the thought experiment of the “brain in a vat”

(Iani 2021; McKeown and Lawrence 2021; Zilio 2022). Yet a converging body of evidence suggests that the very building blocks of thought could be receptor-derived. We argue that to think and imagine is to recombine sensations, replaying or reshaping inputs originally structured by receptor repertoires. Mental imagery provides a direct window into this dependence. Neuroimaging studies show that visual imagery activates early visual cortices, reusing maps originally shaped by retinal receptors (Dijkstra 2024; Chang et al., 2025). Tactile and motor imagery likewise recruit somatosensory and motor areas, themselves established through proprioceptive and mechanoreceptive inputs (Kilteni et al., 2018; Wen et al., 2024; Zhang et al., 2025). Imagination emerges not as an autonomous cortical faculty, but as a recombination of architectures laid down by receptor signals, even when no external input is present. Recent work directly connects receptor physiology with the phenomenology of imagination. Vascular and metabolic activity in visual cortex, mediated by receptor-driven blood flow and oxygenation, predicts not only visual perception, but also the vividness of mental imagery (Sasaki et al., 2024). Studies of motor learning likewise demonstrate that representations of skill are inseparable from proprioceptive receptor feedback, suggesting that even imagined movements are scaffolded by receptor channels (González-Grandón et al., 2021; Parma et al., 2024).

Furthermore, evidence supports the view that cognition and memory formation rely on receptor-driven inscriptions acting as experience-bound traces that guide neural reactivation and long-term encoding. For instance, Huelin Gorriz et al. (2023) show that hippocampal replay during sleep is shaped by prior sensory-motor experience, with novelty and repetition determining memory prioritization. Interoceptive rhythms intersect with volition and attention too. Clinical observations suggest that conscious access to interoceptive streams retunes the weighting of receptor-driven signals in action selection. Dysfunctions in interoceptive receptors and mappings are increasingly linked to anxiety, depression and psychosomatic disorders, reframing them not as purely "top-down" failures, but as disorders of receptor-based coding and prediction (Khalsa et al., 2009). Social life also bears the imprint of receptor channels. Ultrasonic components of infant cries, for instance, elicit hemodynamic changes in mothers' breast regions, a substrate for caregiving that likely depends on specialized interoceptive receptors (Doi et al., 2019). These examples highlight that receptors may shape not only individual cognition, but also relational and affective life.

Uncharted sensors: the speculative possibility of hidden receptors. If imagination is receptor-dependent, its horizons may likewise rest on receptor systems still awaiting discovery. The history of sensory discovery suggests that our catalogue is incomplete. Modalities once thought fixed have expanded: thermoreceptors and mechanoreceptors in mammals were characterized only in recent decades, as well as ammonium has been added as a sixth gustatory quality in humans (Roper et al., 2019). Each discovery has suggested that our definitions of cognition may need continual revision. The natural question follows: might additional receptor systems underlie the most abstract dimensions of thought and imagination?

Several candidates point in this direction. At the metabolic level, receptors monitoring energy states and nutrient flux appear to exert direct influence on memory and decision-making. For instance, glucose, lactate and oxygen sensors shape attention and choice (Li and Freeman, 2015; Schurr 2025; Yang and Yan, 2025). At a supramolecular scale, receptor-like assemblies may act as collective detectors of structural patterns, with the proposal of 'supramolecular phrenology' suggesting that higher-order cognition could arise from receptor complexes beyond classical neurotransmission (Tozzi 2015). Immune receptors detecting cytokines and inflammatory signals are likewise tied to mood and cognition, suggesting that immune sensing may stand for an unnoticed factor able to scaffold thought (Dantzer 2018). Receptor involvement may extend further into immunity and repair. Nociceptor ablation impairs healing, while CGRP release orchestrates neutrophil and macrophage activity, accelerating tissue repair (Lu et al., 2024). Likewise, TRPC5 has been identified as a mechanosensitive ion channel mediating inflammatory mechanical allodynia (Sadler et al., 2021). Pain further illustrates receptor centrality. TRPV1-mediated sensitization drives persistent inflammatory pain, with nociceptor activity sufficient for tactile allodynia (Ghitani et al.

2025). Again, Krause corpuscles act as genital vibrotactile sensors driving sexual behavior (Qi et al. 2024).

Physical accounts expand this horizon into new measurable domains. Research on biological quantum sensing indicates that living systems may exploit quantum-level mechanisms to detect fields, particles or subatomic states (Marais et al., 2018; Kim et al., 2021; Alvarez et al., 2024). For instance, magnetoreception may rely on quantum coherence in cryptochromes, already established as compass receptors in birds as reported before (Smith et al., 2022; Thoradit et al., 2023). Biological sensors based on radical pairs, magnetite crystals or MagR proteins appear to approach quantum limits of energy resolution (Kominis and Gkoudinakis 2025). Receptor repertoires could include channels attuned to physical phenomena far beyond the current sensory canon. The implications are profound: if hidden receptors exist, cognition may be even more porous to bodily and physical processes than currently recognized, grounded in molecular, metabolic, immune and perhaps quantum capacities of receptor systems.

To think differently is to sense differently and additional senses may yet await discovery. In the next chapter, we turn to comparative biology, examining how divergent receptor repertoires across species may generate distinct cognitive worlds.

Chapter 6. Species-Specific Repertoires and the Umwelt

If receptors could shape cortical maps and cognition in humans, then they might also define the diversity of experience across species. Each organism inhabits not a single shared reality but a perceptual universe structured by its receptor repertoire. Jakob von Uexküll (1934) called this the Umwelt, i.e., the species-specific world carved out by sensory organs. From this perspective, cognition is not abstract, but grounded in the material specificity of receptor arrays.

Across biology, striking cases illustrate how receptor repertoires generate radically different experiential worlds. The mantis shrimp, with up to sixteen photoreceptor types compared to our three, accesses a multidimensional color space beyond human imagination (Thoen et al., 2014; Donohue et al., 2018). Mosquitoes, whose olfactory receptors are exquisitely tuned to human blood chemistry, inhabit an *Umwelt* in which our scent dominates ecological meaning (Jung et al., 2015). Bats navigate by echolocation, their acoustic receptors transforming echoes into three-dimensional cognitive maps (Goldshtein et al., 2024). Nagel’s question, ‘What is it like to be a bat?’ (Nagel 1974), can thus be reframed as follows: to be a bat is to perceive and imagine through the specialized receptors of echolocation.

Other findings deepen this view. Comparative work shows mosquitoes discriminating between blood and nectar through dual olfactory receptor systems (Jové et al., 2020). Marine mammals illustrate interoceptive adaptation: unlike terrestrial mammals, seals perceive circulating oxygen directly, enabling prolonged dives without drowning (McKnight et al., 2025). Octopuses demonstrate molecular innovation: their chemotactile receptors, derived from nicotinic acetylcholine receptors, evolved hydrophobic binding pockets enabling “taste by touch,” linking atomic-scale receptor adaptation with unique behaviors. Magnetoreception adds another frontier. Sea turtles display two distinct magnetic systems: a radical-pair compass sensitive to radiofrequency disruption and a learned magnetic map sense guiding natal homing (Goforth et al., 2025). Insects extend this variety: Bogong moths combine visual star maps with magnetic sensing to migrate to alpine caves (Dreyer et al., 2025), while debates on Drosophila suggest that overlooked magnetic responses can be reliably conditioned (Kyriacou 2024).

These cases reveal that receptor repertoires are not incidental features, but constitutive determinants of cognition. A fish’s detection of electric fields or a moth’s night navigation are not mere behaviors, but expressions of receptor-driven cognitive maps. Taken together, these findings reinforce that the diversity of cognition across life is rooted in receptor diversity. To understand another species’ mind is to understand its receptor architecture and the *Umwelt* it defines. In the next and final chapter, we outline how receptors, rather than cortex alone, provide the constitutive ground of cognition, imagination and consciousness.

Chapter 7. Conclusion

The traditional picture of the brain situates cognition within cortical and (to a less extent) subcortical networks, relegating receptors to passive portals. Across this review, we have argued for a reversal of this hierarchy toward a receptor-centered approach. Receptors are not secondary to cognition, but constitutive of it. They shape cortical maps, determine imaginative capacities, ground our sense of body and world and define the cognitive possibilities of living species. The cortex can be best understood not as the origin of thought, but rather as a plastic substrate inscribed by receptor repertoires, a view supported by the large body of evidence we have reviewed.

A challenge to receptor primacy is the claim that cortical protomaps can emerge prior to sensory input. Antón-Bolaños et al. (2019) showed that thalamic calcium waves generate an embryonic scaffold of the mice's somatosensory cortex even in the absence of peripheral stimulation. Similarly, Guillamón-Vivancos et al. (2022) demonstrated that early retinal waves help segregate visual and somatosensory circuits in the superior colliculus during a critical developmental window, shaping modality-specific connectivity before sensory experience. At first glance, these findings appear to weaken our receptor-centered account, suggesting that intrinsic neural activity alone can establish the blueprint of cortical organization. Yet a closer look reveals that this "spontaneous" activity is not truly independent of receptors. Thalamic calcium waves depend on ion channels (i.e., molecular receptors transducing intracellular dynamics), while retinal waves are inseparable from the excitability of photoreceptor-linked circuits. What is described as "intrinsic" activity is thus still receptor-based at the molecular level. More importantly, these embryonic protomaps are provisional. Without postnatal receptor-driven input, they fail to stabilize, refine and mature into functional sensory representations. This suggests that prenatal activity sets the stage and receptors write the play.

Another challenge concerns the frequent argument that the generativity of mathematics exemplifies forms of abstraction transcending receptor input. Nevertheless, mathematical cognition appears grounded in receptor-derived spatial systems. Meta-analytic work by Li et al. (2025) shows that logical–mathematical symbol processing shares strong neural overlap with spatial cognition, revealing a sensorimotor substrate for logic and reasoning. Similarly, Amalric and Dehaene (2017) demonstrate that professional mathematicians recruit bilateral intraparietal and ventral temporal regions, i.e., areas linked to perceptual magnitude and visuospatial mapping rather than perisylvian language zones, confirming that mathematical thought may recycle receptor-shaped spatial architectures for abstract reasoning.

Still, it could be argued that chimpanzees, phylogenetically close to humans, display different cognitive abilities despite possessing similar receptors. This is not the case, since receptor repertoires differ between the two species, particularly in number and distribution. For instance, chimpanzees exhibit a distinct arrangement and distribution of muscles of facial expression compared with humans (Burrows et al., 2006; Domínguez-Oliva et al., 2024), leading to substantial differences in the density, type and spatial organization of proprioceptive receptors across the facial region. And this difference in receptors' repertoire, according to our hypothesis, is one of the factors capable of explaining the cognitive differences between the two species.

Limitations. A receptor-centered model must acknowledge that cognition is not exhausted by sensory input. Higher functions like memory consolidation, symbolic reasoning and language involve recursive processes that cannot be fullyreduced to receptor activity alone. Long-term memory depends on molecular mechanisms of synaptic plasticity, including protein synthesis and dendritic remodeling, which transcend operations of receptor systems. A further challenge lies in distinguishing receptor-driven processes from emergent cortical dynamics. Neural oscillations, attractor states and large-scale synchronization can exhibit properties that appear detached from specific receptor inputs. Teasing apart when cognition is receptor-grounded and when it is self-sustaining will require experimental approaches tracking receptor activity and cortical dynamics simultaneously. Genetic manipulation can isolate or silence receptor classes, yet the systemic compensations that follow may obscure causal roles. High-resolution imaging techniques, such as

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cryo-electron microscopy or in vivo two-photon imaging, provide exquisite structural detail but struggle to capture dynamic receptor ensembles across whole networks. Electrophysiological methods reveal real-time activity, but cannot easily distinguish receptor-level contributions from downstream circuit effects. Cross-species studies are plagued by interpretive difficulties, since receptor repertoires may be conserved yet serve divergent functions in different ecological niches.

Finally, several conceptual limitations warrant acknowledgment. A receptor-centered model may verge on reductionism if construed too narrowly, risking the interpretation that receptors alone determine cognitive architecture. This approach could neglect the higher-order modulations exerted by cultural, ecological and semiotic systems, whose recursive interactions with receptor-driven dynamics are essential for the emergence and diversification of complex cognition.

Applications and predictions. A receptor-centered model has wide-ranging implications across diverse fields, including medicine. Patients who lose proprioception illustrate how the collapse of receptor input forces reliance on vision, reshaping both motor coordination and higher-order cognitive capacities (McNeill et al., 2008).

Receptor dysfunction may play a central role in the pathophysiology of depression. Disruption of NMDAR- and AMPAR-mediated transmission compromises BDNF-dependent synaptic plasticity, while altered glucocorticoid receptor signaling contributes to stress-induced vulnerability (Francija et al. 2019; He et al. 2023; Freudenberg et al. 2025). Dysregulation of serotonergic 5-HT1A and GABAAα2 receptors further disturbs the excitatory–inhibitory balance, diminishing dopaminergic efficacy. In addition, “non-classic” receptors, including metabotropic glutamate, opioid and insulin receptors, are emerging as potential therapeutic targets, strengthening the receptor-based framework for understanding depression (Wang et al. 2021). These examples suggest that receptors could stand for a privileged therapeutic target, with modulation at this level capable of reorganizing entire domains of cognition and behavior.

The next decades are likely to reveal receptor systems redefining our conception of mind as radically as the discovery of new sensory modalities did in the past. Several directions can already be anticipated. (1) Novel metabolic receptors might link nutrient sensing directly to cognition, clarifying how energy availability could shape perception and decision-making; (2) Immune receptors could emerge as mediators of direct communication between systemic inflammation and mood, reframing psychiatric disorders as immunoreceptive imbalances; (3) Supramolecular receptor complexes might prove central to integrating large-scale biochemical states into neural coding; (4) Quantum-level receptors, akin to cryptochrome magnetoreception, could allow detection of fields or particles hidden to current biology; (5) Advances in synthetic biology, nanotechnology and receptor engineering might open new avenues for expanding human cognition beyond its natural limits. Artificially designed receptors, generated through protein engineering or nanoscale technologies, could be integrated into the nervous system, extending the human sensory repertoire into synthetic domains such as radiation detection or molecular-scale chemical mapping. Sensory augmentation might allow perception of ultraviolet light, geomagnetic fields or chemical gradients, reshaping imagination, reasoning and conceptual frameworks.

Other possibilities include (6) Mechanoreceptors in skeletal and connective tissues could regulate higher-order decision-making through continuous interoceptive feedback; (7) Receptor systems for microbiome-derived metabolites could link symbiotic ecosystems directly to cognition; (8) Receptor-level oscillatory might be coupled at subcellular or mitochondrial scales to bridge bioenergetics and computation, providing a theoretical substrate for consciousness grounded in metabolic flux; (9) Neuroprosthetics could advance beyond cortical decoding toward direct receptor-level interfacing, enabling artificial limbs to restore fine tactile, thermal and proprioceptive feedback with biological precision; (10) Connectomics might be extended to encompass receptor architectures, thereby capturing cognition as a continuous process spanning molecular, cellular and systemic scales; (11) Artificial intelligence could be advanced through receptor-level modelling, where bio-inspired algorithms grounded in receptor coding may allow systems to learn, adapt and generalize according to the sensory principles that organize biological cognition.

Future neurosciencee will turn from mapping circuits alone to discovering, classifying and engineering receptor repertoires. The next breakthroughs may come less from functional imaging than from receptor biology: transcriptomic mapping of peripheral neurons, optogenetic manipulation of novel receptor classes and integration of receptor-level signals into connectomic models. Cognition, in this view, is not software running on cortical hardware, but rather the living product of receptor architectures continually inscribing the brain. We are, in the most literal sense, our receptors.

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