Wider than the Sky: An Alternative to "Mapping" the World onto the Brain

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Abstract: This paper reevaluates the conventional topographic model of brain function, stressing the critical role of philosophical inquiry in neuroscience. Since the 1940s, pioneering studies by Penfield and subsequent advancements in visual neuroscience by Hubel and Wiesel have popularized the concept of cortical maps as representations of external and internal states. Yet, contemporary research in various sensory systems, including visual cortices in certain animals, questions the universal applicability of this model. We critique the restrictive influence of this paradigm and introduce an alternative conceptualization using the olfactory system as a model. This system's genetic diversity and dynamic neural encoding serve as a foundation for proposing a rule-based, adaptive framework for neural processing, akin to the dynamic routing in GPS technology, which moves beyond fixed spatial mappings.

Keywords: *Philosophy of neuroscience, topographic paradigm, representational drift; olfaction, sensory coding, genetic transcription, morphological computation, pluralism*

The Brain—is wider than the Sky—
For—put them side by side—
The one the other will contain
With ease—and you—beside—
(Emily Dickinson, 1862)

1. Introduction

In the 1940s, Wilder Penfield discovered during neurosurgeries that stimulating small portions of the brain would elicit characteristic responses in patients. In 1951, Penfield published his now-famous homunculus, which would become an iconic symbol of brain architecture. This was the beginning of an idea about brain architecture that has dominated neuroscience research, to the nearly complete exclusion of all other possibilities, - at least until the last few

years. Work on cortical columns and visual representation by Vernon Mountcastle (Mountcastle et al., 1957), David Hubel and Torsten Wiesel (1959; 2004) —awarded a Nobel prize for their work in 1981—, and their later computational counterpart David Marr (1982), gave further support to this idea of a neural "representation" of the world mapped onto brain space. These influential reports further propelled this research program (Shepherd, 2009; Haueis, 2016), which now involves many laboratories and thousands of post-docs and graduate students, using increasingly refined neuroimaging techniques on genetically engineered and highly homogeneous model organisms. Even the occasional inexplicable result—for example, many animal cortices do not possess a columnar organization (Naumann et al., 2015; Laurent et al., 2016; Fournier et al., 2018) —has not slowed the research effort or diminished the idea that the brain represents the outside world by constructing a map in three-dimensional neural space.

Lurking just below the surface, and carefully sidestepped by the experimental community, is the troubling question of who is actually making sense of such a cortical roadmap. Is there a tiny executive homunculus watching the visual, acoustic, somatosensory, and other sensory maps and sending out instructions to muscles in accordance with the picture of the world it is receiving? Surely, no one subscribes to this; the homunculus appears as an ancient and silly idea today (Dennett, 1993). But then, who *is* reading the map? Or why construct a map if we discard its reader?

This is a profoundly philosophical question, and ignoring it has led to years of scientific effort chasing down a singular model that now seems to be in need of substantial revision, assuming it is worth preserving at all. It is one example of the perils of ignoring philosophical questions when they might upset an admittedly large cache of experimental data. It is also a cautionary tale about the severely monistic approach modern science takes to many of its most fundamental problems. Other alternatives were and are available as possible models. Data from other than the predominant systems (cats, monkeys, humans) could have suggested alternative models that were never imagined, let alone ignored. Instead, the work of Hubel and Wiesel and the Nobel committee's recognition directed brain research along an overly narrow path for 50 years.

This paper exemplifies the fecundity of philosophical analysis in current neuroscience by demonstrating how it can lead to a deeper and alternative understanding of brain function, promoting a shift away from rigid paradigms towards a more pluralistic and integrative approach in neuroscience. Our argument unfolds as follows: We start by delineating the kernel of the topographic paradigm in its origin, implications, and challenges. Section 2 examines the historical development of the topographic model in neuroscience, influenced by the work of Hubel and Wiesel. Section 3 explores the limitations of this paradigm, especially considering findings in the olfactory system, which lacks spatial organization and shows dynamic, experience-dependent neural encoding. Next, we examine why olfaction serves as a valuable model system for neuroscience, highlighting its potential to provide a robust framework for developing an alternative model of sensory encoding. Drawing on philosophical discussions regarding the genesis of scientific knowledge, section 4 discusses how olfaction can significantly inform general neuroscience. Section 5 puts this theoretical argument into practice with an alternate account of sensory information encoding that is guided by genetic transcription mechanisms that modify responses according to environmental and experiential factors. This account demonstrates how sensory systems employ rule-based mechanisms to process data dynamically, eliminating the requirement for spatial maps or static neural representations. Against this backdrop, we conclude with the implications of olfactory research for other sensory systems, urging the development of a more flexible paradigm in neuroscience. This approach should strive for broad applicability as well as carefully accommodate the unique characteristics of different systems, enhancing our holistic understanding of neural function.

2. Historical Background: The 'Visualization' of Modern Neuroscience

The prevailing model of sensory cortices presents us with a blueprint of a beautifully systematic correlation between sensory inputs and the hierarchical, spatial patterning of neural activity. This principle has delineated the paths of vision and audition with deceitful clarity. How does the brain translate a raw cacophony of light and other sensory inputs from the external world into a coherent perceptual narrative? This question monopolized neuroscientific discourse for most of the twentieth century (Shepherd, 2009). Sensory systems, as complex networks of

cells, capture the world in patterns both spatial and temporal, creating perceptual imagery from the language of neural firings.

In the late 1950s, a serendipitous discovery promised to shed light on this issue. Hubel and Wiesel (1959; 1960; 1961; 1962; 1963; 1965; 1969), postdocs in Stephen Kuffler's (1953) laboratory, embarked on a series of experiments involving the visual cortex. Their initial forays, monitored through microelectrodes delicately placed in the V1 region of the cat cortex, yielded a striking finding: it was not just any stimulus that these cells responded to, but lines, particularly lines in specific angles and orientations. Neurons, with approximate responses to visual input, cluster together, creating a cellular map of preferences and inclinations. Hubel and Wiesel's (2004) research suggested that visual system processing is a hierarchically coded reconstruction of input, a complex computation performed by the neural apparatus.

In the wake of Hubel and Wiesel, neuroscience experienced a paradigm shift that can be attributed to two reasons. First, their model of cortical processing began to unify an assortment of disparate single-cell recordings into a coherent whole. Instead of tracking signals from cell A to their projection in cell B, these studies indicated the design through which the visual system transmuted raw stimulus data into three-dimensional objects (Hubel, 1988). Their findings revealed that visual representations were not the result of a homogeneous contribution from individual neurons, as previously been assumed (e.g., McCulloch and Pitts, 1943; Piccinini, 2004), but specialized clusters of cells working together. Second, their research laid the groundwork for a methodology that successfully directed future investigations. This hierarchical, nested paradigm of visual processing—occasionally stretched to its limits (as evidenced by instances such as grandmother cells; Barwich, 2019a)—provided a fresh perspective on the structure of the brain, prompting Marr (1982) to contemplate the exact computations it carries out and inspiring his influential three-stage model of visual object construction (Bickle, 2015). It was difficult not to be enamored by the apparent logic of the visual system (figure 1).

It seemed almost inevitable that this reasoning would prevail following Tootell et al. (1988). By employing radioactive glucose, they investigated metabolic activity in the striate cortex of monkeys, observing how different areas of this region responded to specific segments of the

visual field. A critical element emerged: retinotopic mapping, where the visual cortex mirrors specific areas of the retina, creating a precise correspondence between the origin of visual signals in retinal cells and their cortical destination.

Research on other sensory systems, specifically audition, initially echoed these findings in vision, showcasing a comparable organization (Chittka & Brockmann, 2005). The tacit assumption that guided models of cortical maps across sensory systems is that certain brain regions or cell populations consistently exhibit patterned responses to environmental stimuli. The topographic paradigm in neuroscience was cemented.

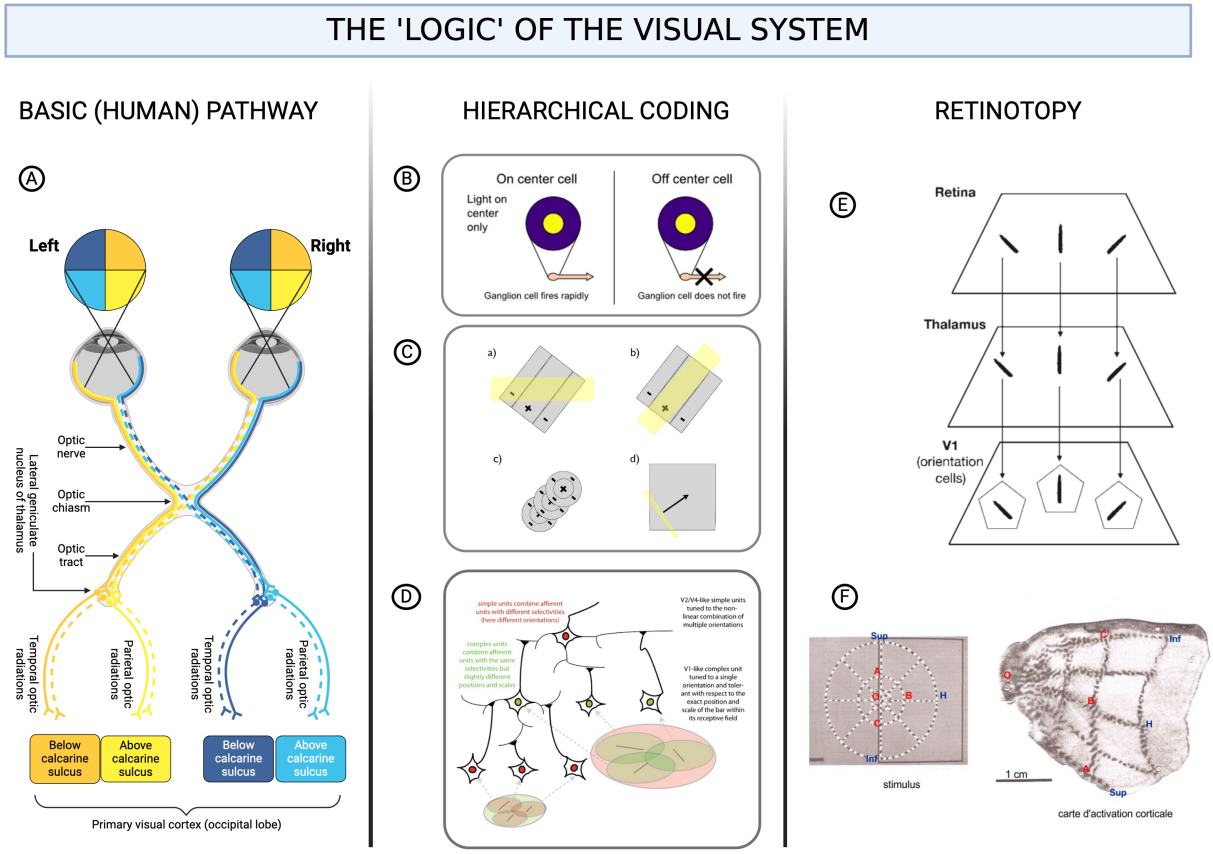

Figure 1 (Barwich, created with BioRender): The 'logic' of the visual system after Hubel and Wiesel. *(A) Schematic anatomy of the (human) visual pathway from retina to thalamus to striatum. (B) Kuffler's Center surround (On- and Off) Cells detecting contrast by being activated when light hits the center of their receptive field and inhibited when light hits the surrounding area, or vice versa (image: Wikimedia, Nneonneo, 2009); (C) Receptive field of a neuron in the V1, hierarchically integrating signals from the retina and LGN/thalamus (image: Wikimedia, Kyle.wg3139, 2013); (D) Receptive field integration:*

hierarchical processing of visual information through increasingly complex 'representations' of neuronal input at successive levels of the visual system (image: Scholarpedia, Thomas Serre, 2015); (E) Extremely simplified principle of retinotopy: mapping of visual input from the retina to corresponding locations in the visual cortex, preserving the spatial organization of the visual scene (image: Barwich, 2020a); (F) Tootell et al.'s 1988 detailed map of the visual striatum highlighting the retinotopic organization of visual field representations in the cortex (image: Wikimedia, Pancrat, 2011).

Revolutions, once they dominate the discourse, can end up in tyranny, though. Science, as we know, does not stick to a script (Medawar, 1963; Schickore, 2008; Firestein, 2012; 2015), and brain research soon revealed unexpected complications beneath ostensibly orderly maps.

Neural processing is not a one-way street. For example, recent insights into the motor strip and auditory cortex cast doubt on the tidy models of topographic organization. Finding multiple body mappings within the motor strip (Gordon et al., 2023) and a columnar architecture of the auditory cortex distinct from that observed in visual or somatosensory systems (Linden & Schreiner, 2003) invite reassessments of the old paradigm. These studies are not isolated incidents but emerge as signs of a larger need to reevaluate topography as the primary organizational principle governing neural activity, with cracks beginning to show also in the conventional model of vision (Livingstone et al., 2017). Non-topographic models for sensory neuroscience are thus gaining interest (Rayner, 1998; Spivey, 2008; Tanenhaus, Spivey-Knowlton, Eberhard & Sedivy, 1995).

We contend that incorporating insights from olfaction, a model system that has been overlooked until now, could greatly enhance current trends toward a reevaluation of sensory coding.

3. Contemporary Developments: Neuroscience 'Olfactorized'

The sense of smell presents an intriguing challenge to conventional approaches in neuroscience, most notably the topographic paradigm. While olfactory signaling appeared to

follow a pattern similar to a well-organized stimulus-feature map, a markedly different picture emerges upon closer inspection (Barwich and Severino, 2023).

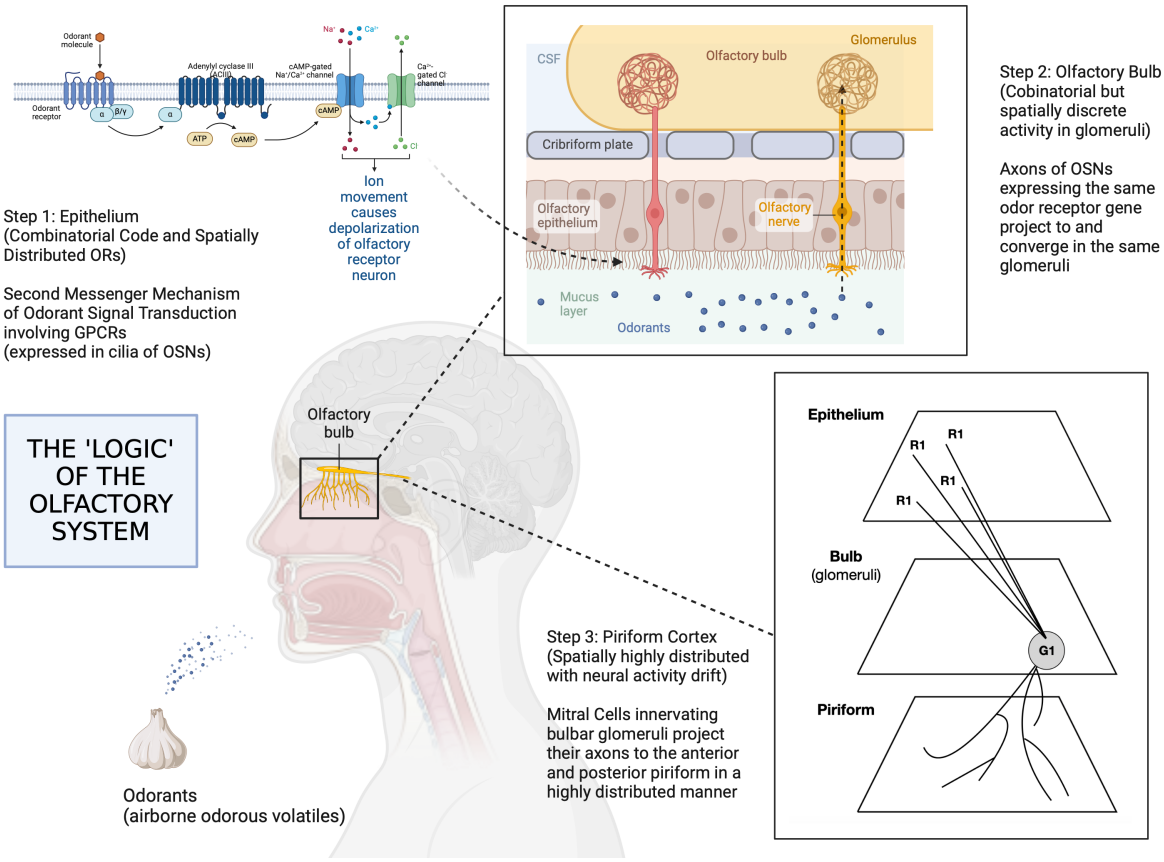

Figure 2 (Barwich, created with BioRender): Basic three-level route of the olfactory pathway. *The olfactory pathway begins with odorant molecules binding to receptors in the nasal epithelium, sending signals via the olfactory nerve to the olfactory bulb. From the olfactory bulb, the signals are relayed to the olfactory cortex and other brain regions such as the amygdala and hippocampus for integration, processing, and perception of smells. (Image in step 3: Barwich, 2020a) Not depicted is the intricate circuitry of granule cells, mitral cells, and various types of interneurons in the olfactory bulb, creating complex processing patterns of excitation and inhibition in the olfactory bulb (see Shepherd and Greer, 1998; Shepherd, Chen, and Greer, 2005; Kay and Sherman, 2007).*

The olfactory pathway presents a *deceptively* shallow three-level route from the air to the cortical core (Firestein, 2001): Two synapses connect epithelial sensory neurons to piriform, the largest area of the primary olfactory cortex (figure 2). Odor processing kicks off with the molecular receptors, olfactory GPCRs—the largest multigene family in the mammalian

genome—expressed in the cilia of sensory neurons (Buck and Axel, 1991; Shepherd, Singer, and Greer, 1996; Firestein, 2005; Kurian et al., 2021). Upon encountering a wide variety of chemical structures, this interaction triggers signals that are then sent to and organized within the glomeruli of the olfactory bulb (Mombaerts et al., 1996), located in the inferior frontal lobe. The bulb displays, or appears to display, a unique activation pattern for every odorant, like an olfactory fingerprint, in contrast to the spatially widely dispersed receptors in the epithelium (Shepherd, 2012; Lodovichi, 2021). Following the lead of the visual system, it was assumed that such spatially discrete activity in response to odorants within the bulb would persist into the piriform cortex, possibly beyond.

But this notion has been radically upended in the last decade, and it matters why that is the case (Barwich, 2020a). Three factors are at play here: the encoding of stimulus properties at the receptor sheet, the genetic and developmental basis of the olfactory bulb, and the phenomenon of "representational drift" found in piriform cortex. Taken together, these factors compel us to reconsider the topographic principle adopted from vision.

3.1 Patterns in the Olfactory Bulb are not Topographic

We must begin with the bulb. The seemingly orderly spatial arrangement of odor signals suggested a topographic principle might govern odor processing, much like retinotopy in vision or tonotopy in hearing (Mori and Yoshihara, 1995; Zu, Greer, and Shepherd, 2000; Uchida et al., 2000; Mori et al., 2006). Yet, this initial assumption—that the olfactory bulb organizes odors or its physicochemical input through a stereotypic, topographic scheme—calls for a thorough reevaluation (Zou, Chesler, and Firestein, 2009). This is largely because the arrangement of glomeruli is neither predictable nor static, but dynamic, diverging significantly from a rigid genetic blueprint.

Consider first *the argument from function*: An explication of what glomerular activity actually "represents" quickly dashes hopes for topographic models in olfaction. When we consider the functionality of the olfactory bulb, we might initially expect each glomerulus to serve as a clear-cut representation of specific odor receptors, much like pins on a map. Each glomerulus serves

as a converging point for the axonal projections of sensory neurons, which typically express a single odor receptor gene (Mombaerts et al., 1996). This arrangement indicated that glomeruli reflect the activity of their corresponding receptors, following the widely held "one gene-one neuron" doctrine,[1] suggesting a clear, structured odor activity map in the bulb. This neat arrangement would certainly simplify the brain's daunting task of decoding smells. Nevertheless, this idea might be more of a logician's wishful thinking than neurobiological reality.

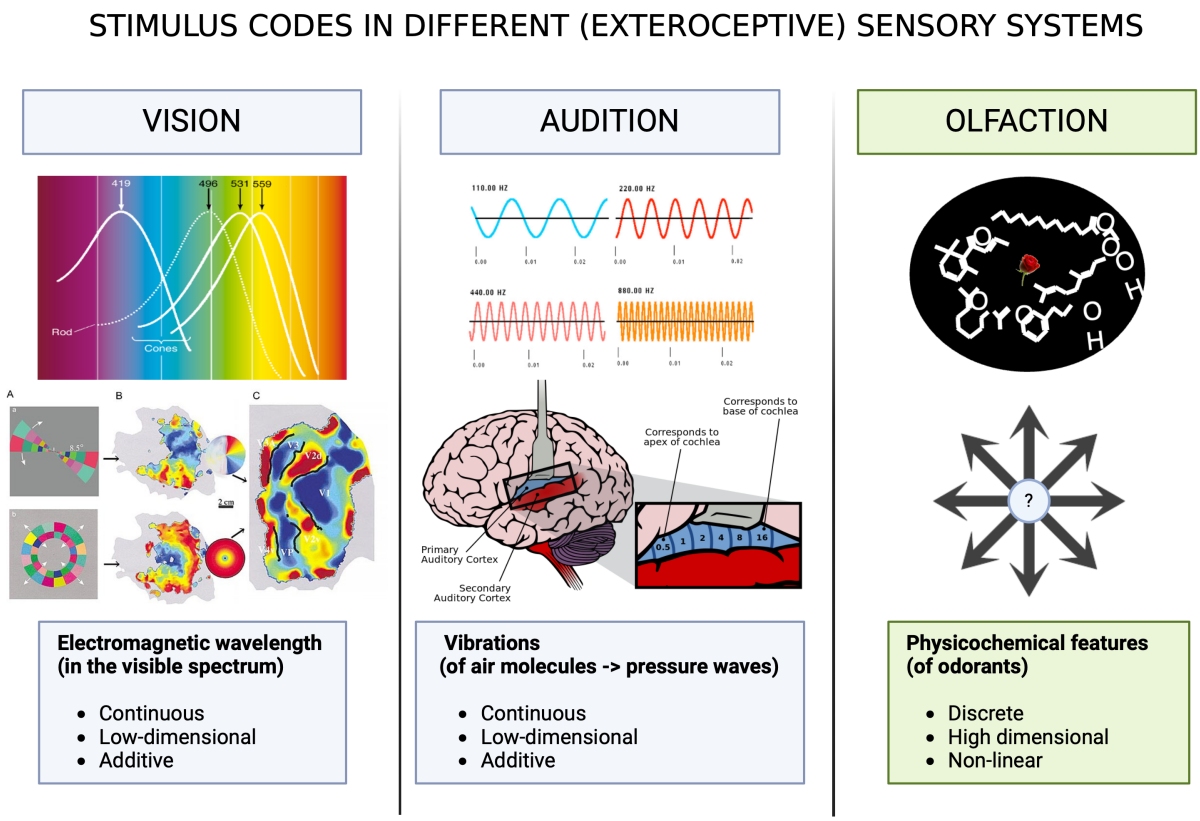

Figure 3 (Firestein and Barwich, created with BioRender): Stimulus codes in different exteroceptive sensory systems. *Left: Color vision involves electromagnetic wavelengths in the visible spectrum, mapped onto neural space via retinotopy (bottom image: Wikimedia, LordFarkquaad, 2013). Middle: Audition processes air molecule vibrations (pressure waves), mapped onto neural space via tonotopy*

[1] Mombaerts (2004) subsequently reexamined this doctrine, proposing a different model that posits an initial developmental stage, characterized by oligogenic expression, which is subsequently refined through processes of positive and negative selection, ultimately leading to cells that typically express a single receptor.

(bottom image: Chittka and Brokmann, 2005). Right: Olfaction deals with discrete and non-linear physicochemical features of odorants, which are not mapped onto neural space through a similar principle like 'chemotopy' or 'odotopy' (top image: Firestein).

One issue with the notion of topographic stimulus-representation in olfaction pertains to the constitution of the distal stimulus itself. In contrast to the low-dimensional continuums of vision and audition, the olfactory system engages with a complex array of high-dimensional stimuli (figure 3). 'Odorants' are not uniformly segmented or arrangeable in sequential physical chunks like the specific ranges of electromagnetic wavelengths processed by the retina's color cones. Instead, odorants comprise thousands of physicochemical properties involved in ligand-binding, forming a rich, combinatorial array of discrete data patterns (Keller and Vosshall, 2016; Poivet et al., 2018; Barwich and Lloyd, 2022). Traditional sensory models, designed for hierarchical and topographic data organization, prove inadequate for this task: If we adhere to these modeling principles, the olfactory system soon would be exhausted its capacity to generate unique activity patterns. This critical aspect, though vital, has been largely overlooked by biologists but would be readily apparent to systems engineers accustomed to managing multidimensional data.

Another issue concerns the functional information contained within the proximal stimulus—that is, the information encoded by odor receptors and converted into neural signals. What precisely do these receptors detect? Odor receptors are notoriously promiscuous, not monogamous; they engage combinatorially with a variety of physicochemical features, rather than responding to singular stimulus properties (Malnic et al., 1999).[2] The combinatorial nature of these activations throws a wrench into any simplistic, one-to-one mapping we might hope to draw because odor receptors are *feature-selective* but not *feature-specific* (Barwich, 2022).[3] A single receptor can respond to diverse features across different odorants: it may react to the topological polar surface area of one odorant (O1), a functional group in another odorant (O2), and the specific ring size in yet another compound (O3).—Plus, the case of mixture perception,

[2] See also an earlier study (Firestein, Picco, and Menini, 1993) and another Ma and Shepherd, 2000.
[3] Ross (2021) examines the concept of specificity in causal relationships, focusing on value specificity, which refers to the range of effects a single cause can produce. This means that while odor receptors are selective in their responses, they are not limited to responding to only one specific feature or type of feature.

involving modulation mechanisms, further complicates this picture (Reddy et al., 2018; Xu et al., 2000; de March et al., 2020; Inagaki et al., 2020; Pfister et al., 2020; Zak et al., 2020; Barwich, 2020a, 2021a; Barwich and Xu, 2021; Kurian et al., 2021; Xu, Zou, and Firestein, 2023).[4]— Given the inherent ambiguity in receptor coding, we must ask: What does a glomerulus actually "represent", if not just the feature-underdetermined signals from its receptor?

Briefly comparing olfaction to vision to summarize this *argument from function* illuminates their distinct governance. Unlike the cells in the primary visual cortex, which selectively respond to specific orientations, olfactory glomeruli handle a broad spectrum of physicochemical features. Despite initial appearances of selectivity, odor receptors are not feature-specific; they respond to a range of physicochemical properties through combinatorial coding. This indicates a lack of a straightforward, predictable feature-map within the bulb based on receptor activity.

Second, consider the *argument from development*: The organization of the olfactory bulb is notably flexible, challenging the traditionally more rigid topographic model. Glomeruli within the bulb form adaptively, not stereotypically, during development, shaped by both environmental and genetic factors. Research that tracks alterations in axonal connections and variations in odor receptor gene expression confirms the flexible, dynamic structure of olfactory organization (Zhou, Chessler, Firestein, 2009).

A series of studies on sensory neurons involving various substitutions and modifications of receptor genes demonstrates that the organization of glomeruli within the olfactory bulb is not as rigid and uniform as previously thought (figure 4). For example, by replacing one receptor gene with another—such as swapping the mOR23 receptor gene (OlFR16) into the spot of the m71 receptor gene (OlFR151)—we see the creation of cells that send their axons to a different glomerulus than those expressing the original m71 or mOR2310 receptors. Feinstein et al. (2004) modified mice linking GFP with OR receptor genes to see if neurons with altered genes would still target the mOR23 or m71 glomerulus, supporting the hypothesis that receptors

[4] Suggested allosteric modulation in odor mixture coding (Xu et al., 2020): For instance, receptor R1 may cease to respond to odorant O1 when it is accompanied by odorants O2 and O3, while receptor R2 may only respond to O2 in the presence of O1 and O3, yet not in isolation.

guide axons to their genetic targets. Contrary to expectations, these modified neurons formed new glomeruli in unexpected locations instead of converging on the parental OR glomeruli. Further experiments replaced odor receptor genes with non-olfactory ones, such as an ß-adrenergic receptor (Feinstein et al., 2004), or knocked out receptor genes entirely in some neurons (review: Zou, Chesler, and Firestein, 2009; context: Barwich, 2020a, Ch. 7).

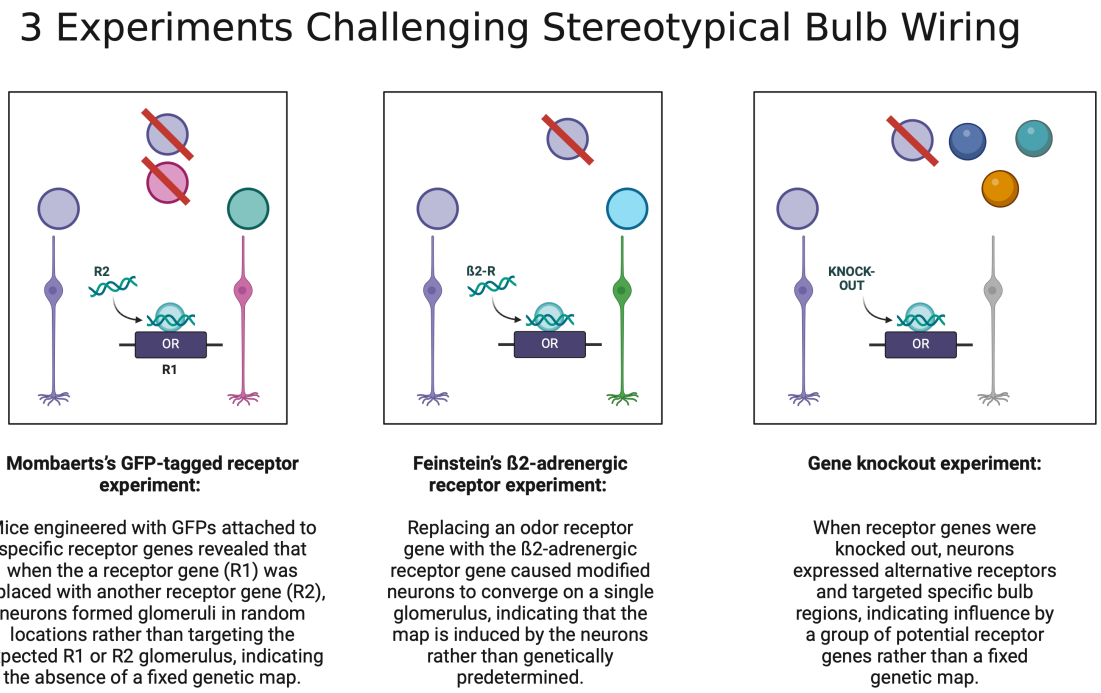

Figure 4 (Barwich, created with BioRender): Stimulus codes in different exteroceptive sensory systems. *The figure illustrates the principles of three experiments undermining stereotypic topography in the olfactory bulb, suggesting the olfactory map is dynamically organized by neurons rather than genetically prewired. (In Feinstein et al., 2004; reviews in Zou, Chesler, and Firestein, 2009; Barwich, 2020a, Ch. 7)*

In this light, the olfactory bulb's architecture stands in stark contrast to that of vision. This functional analysis reveals that activity within the bulb is not tied to specific features, indicating an absence of 'chemotopic' or 'odotopic' organization—that is, it doesn't map physicochemical features in a manner akin to how visual systems map features and orientations via selective cells. Developmental evidence further supports this divergence (Zou et al., 2004), indicating

that the organization of glomeruli does not follow a fixed pattern conducive to odor signal mapping analogous to retinotopic mapping in vision.

In olfaction, the precise functional mapping from receptor cells to specific locations in the olfactory bulb remains elusive. Although there is a clear link between OSN receptors and their axonal destinations in the glomeruli, this pattern might not directly correspond to a functional representation of olfactory features. Instead, it may constitute a developmental solution to the complex problem of connecting thousands of axonal populations to the brain. Such developmental arrangement might require a reappraisal considering its own functional significance. This insight aligns with the many philosophical challenges to the traditional biological and neuroscience tenet that structure dictates function (Allen, Bekoff, and Lauder, 1998). This tenet often fails under closer evolutionary examination, particularly considering phenomena like exaptation, where features developed for one purpose are co-opted for another (Gould, 1985). History in biological sciences consistently shows many structures initially perceived as functional are byproducts of evolutionarily determined developmental necessities.

Overall, these insights shift our understanding of bulbar activity patterns from a deterministic, principally stimulus-driven to a more probabilistic developmental perspective on the neural architecture and information processing in olfaction (Cleland and Sethupathy, 2006).

3.2 Representational Drift in the Piriform Cortex

When placed alongside received models of the visual and auditory systems, olfaction presents a contrast. While the former systems show a degree of organizational consistency and structure in their sensory mappings, olfaction eschews this approach, favoring a more fluid and less predictable strategy. This plasticity in neural encoding becomes most apparent within the piriform cortex.

The piriform cortex, far from presenting an orderly neural territory, showcases its complexity through what appears to be a chaotic, non-target driven domain (Stettler and Axel, 2009;

Sosulski et al., 2011; Chen et al, 2014; Diodato et al., 2016; Roland et al., 2017). Conventional sensory maps, like those observed in vision and hearing, depict a structured and consistent correlation between the external world and neural representations. In contrast, the organization—or conspicuous disorganization—of the piriform cortex reflects an adaptive strategy finely attuned to the unpredictable dynamics of olfactory stimuli, tailored to a sensory environment marked by a high degree of molecular diversity and environmental variability. Variables such as air currents and humidity significantly influence how odors are perceived and processed (Philpott et al., 2004), necessitating a system that prioritizes flexibility over rigid mappings. Despite the seemingly random distribution of axonal projections (figure 5, left), the piriform cortex adeptly synthesizes signals from various brain areas, forming variable activity patterns throughout olfactory information processing (Cohen et al., 2015; Wilson and Barkai, 2018; Li and Wilson, 2024). It emerges as a pivotal hub, linking memory, emotion, and decision-making (Barwich, 2020a, Ch. 8), thereby illustrating a sophisticated dynamic interplay that underpins its role in sensory processing.

A striking aspect of the piriform cortex's functionality is its exhibit of representational drift (Schoonover et al., 2021). Representational drift is a phenomenon where neural responses to the same stimuli evolve over time, with cell responses gradually shifting (Driscoll, Duncker, & Harvey, 2022; Rule, O'Leary, & Harvey, 2019), defying the expectation of stable neural representation. This finding is not only significant for our understanding of the olfactory system but also challenges the broader assumption across sensory systems that neural responses are inherently stable. This manifestation of drift as neural plasticity, once primarily noted in regions like the hippocampus and posterior parietal cortex (Kentros, Agnihotri, Streater, Hawkins, & Kandel, 2004; Lee, Briguglio, Cohen, Romani, & Lee, 2020; Rubin, Geva, Sheintuch, & Ziv, 2015; Driscoll et al., 2017), was initially thought a marker of cognitive systems. However, drift is now documented in primary sensory cortices as well.[5] This expansion of our understanding of where

[5] Following the findings of Schoonover et al., subsequent publications by Marks and Goard (20221), Deitch, Rubin, and Ziv (2021), and Bauer et al. (2023) uncovered comparable patterns of representational drift in the visual cortices of mice, specifically including the striatum (V1). While we observe notable differences in how this drift presents in the olfactory and visual systems—with the visual system maintaining representations (Keinath, Mosser, and Brandon, 2022)—these discrepancies are not simply curiosities but warrant deeper examination. The varying levels of adaptability observed might be key to understanding how the brain processes sensory information differently across modalities.

and how plasticity occurs suggests a broader, more dynamic capacity for adaptation in neural structures than previously appreciated.

The piriform cortex demonstrates an extraordinarily high degree of drift and adaptability, adjusting its neural codes even in the face of repeated and consistent stimuli. Schoonover et al. (2021) demonstrated that the piriform's response to odorants is neither static nor fixed, but dynamically evolves over time, and does so with startling rapidity. Within just one month, piriform "representations" can undergo profound transformations (figure 5, right). Imagine the neural representation of an odor in early January—say, the distinctive scent of furan (C_4H_4O), an aromatic compound with notes ranging from caramel to smoky and fruity. By the onset of February, its neural 'representation' (i.e., its activity pattern in neural populations) has altered so drastically that it is as distinct from its January version as it would be from an entirely different scent, like musky eugenol ($C_{10}H_{12}O_2$), known for its spicy, clove-like aroma. Crucially, this neural drift continues unabated even with repeated exposure to the same odorant, rigorous daily stimulus training, or even fear conditioning, all of which have minimal effect on curbing the drift.

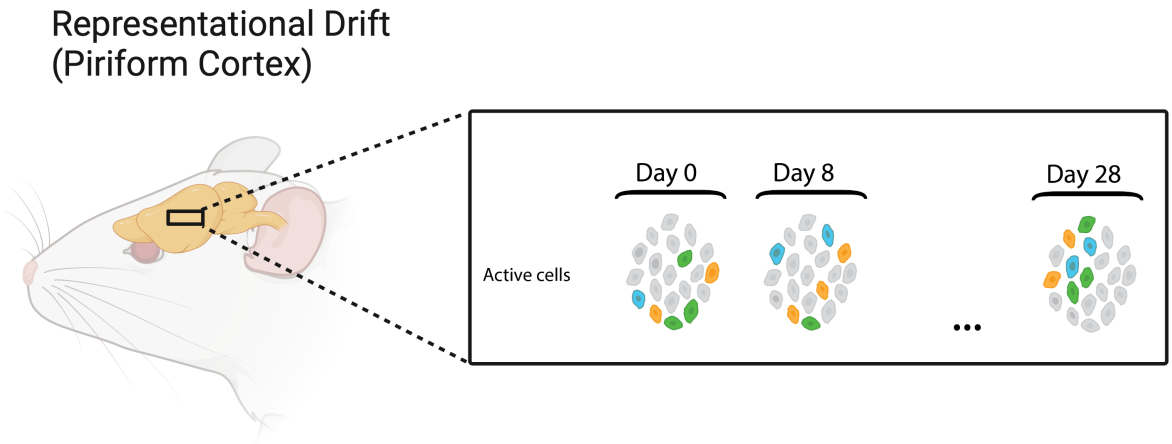

Figure 5 (created with BioRender): Representational Drift in Piriform Cortex. *Neural representations of sensory information evolve over time, with cell responses gradually shifting, challenging the expectation of stable neural representation, even when the external stimulus remains constant. This change, driven by plasticity in neural circuits, can affect the stability and reliability of sensory perception and memory. (Image in box: Barwich and Severino, 2023)*

In summarizing this section, it transpires that the topographic paradigm has markedly delayed, if not hindered our understanding of olfaction by not adequately capturing the sophisticated neural dynamics involved in its signal processing. Especially observations from the piriform cortex compel us to reconsider the principles that govern neural organization. Therefore, it is worth considering that topography may not be a foundational principle of neural organization, but rather a contingent property emerging from the operations of specific systems, influenced by the affordances of stimuli or the functions unique to each sensory modality. This line of inquiry challenges the prevailing paradigms in neuroscience and suggests a shift towards understanding the brain as a highly flexible, context-dependent and associative processing hub.

Thus far, we have explored how the persistence of the topographic paradigm is supported by historical developments and convenience (section 2). Recent advances in sensory neuroscience, particularly in the study of olfaction, are beginning to dismantle the characteristics of the topographic paradigm from which causal inferences have traditionally been drawn (section 3). Beyond this corrective value, we now transition to the second part of our argument, introducing the positive heuristics that arise from incorporating the study of olfaction into broader neuroscience modeling (sections 4 and 5). The remainder of this paper demonstrates that philosophical perspectives on science can be more than just critical—they can be constructive when used complementarily.

4. Philosophical Considerations: Olfaction, a Model for Neuroscience or 'the Odd One out'?

How can a stronger focus on olfaction, and recent insights into its processing, reshape and effectively benefit our approach to neuroscience? Historically, olfaction was routinely dismissed as an eccentric outlier within sensory systems, perceived as offering little of general neuroscientific insight. This perception contributed to its marginalization in terms of funding and attention throughout the twentieth century (Barwich 2020a). However, the landscape of olfactory research transformed dramatically with Buck and Axel's (1991) groundbreaking identification of OR genes, revealing the largest family of G-protein-coupled receptors, GPCRs in short, in the mammalian genome (Buck, 2004; 2005; Axel, 2005; Mombaerts, Firestein, and

Greer, 2014; Barwich, 2020b; 2021b). This discovery not only integrated olfaction into the core of neurobiology and genetics but also highlighted its potential as a distinctive model for both pharmacology and neuroscience (Shepherd, 1991; Barwich, 2015). Considering these advances, it thus is surprising that olfaction remains largely undervalued, with its contributions and significance still not fully acknowledged within mainstream neuroscientific modeling and science education. This oversight exemplifies a broader issue in the field, where entrenched views can obscure emerging insights and hinder the recognition of valuable research avenues.

Indeed, olfaction continues to face a paradoxical dilemma. On one hand, if smell is viewed as too analogous to vision, skeptics argue that it offers little new, given the advanced state of vision science. On the other hand, if it is considered too distinct from vision, critics claim it lacks broader relevance, confined to illuminating only its peculiar mechanisms. This predicament raises a pivotal question: What is the value of spotlighting and embracing olfaction as a model system in broader neuroscience? This issue highlights a core tension within scientific paradigms—the interplay between the quest for new knowledge and the assimilation of this knowledge within established scientific frameworks. Olfaction, residing at the border of similarity and distinctiveness, compels us to reflect on our conventional notions of what makes a scientific model valuable and relevant and reconsider the criteria by which scientific utility is judged.

We offer two strategies to navigate this dilemma, beginning with an endorsement of *scientific pluralism*. Not long ago philosophers of science offered a vision of science that discovered lawful generalities whose power was directly related to their ability to offer unifying explanations over a wide domain of phenomena (Cat, 2024). As philosophers began to consider biology and even physics more carefully their visions of a unified science began to give way to a more complex account of science where piecemeal integration replaced universalizing unification (Giere, 1988; 2006). This pluralistic vision of science does not seek or expect single answers. Grounded in an appreciation for the multiple methodologies of science, the diverse perspectives of scientists, and the incredible variety within and between species in the biological sciences, pluralist accounts of science lead us to expect and value conflicting models whose results may not be easily reconciled (Feyerabend, 1974; Cartwright, 1999; Kellert, Longino, and Waters, 2006; Wimsatt, 2007; Mitchell, 2012; Chang, 2012). Importantly,

pluralism does not suggest that these diverging approaches lack scientific robustness or fail to accurately account for real properties or causes in the world (Dupré, 1993; Massimi, 2022). Often, the discernment of structural and causally relevant relations depends significantly on the conceptual framework employed (Barwich, 2013). For example, the classification of chlorine and its isotopes as one kind or several, based on either their electronic or nuclear structure, varies with the context of inquiry (Barnes, 1982). When applied to neuroscience, the use of multiple model systems for building sensory processing models broadens our understanding of the phenomena at hand—regardless of how similar or dissimilar olfaction may be to vision.

Alongside embracing scientific pluralism, another response is to mind *the evolution of scientific paradigms*, considering how precisely the blend of similarities and differences across various model systems drives theoretical and empirical advancements in understanding scientific phenomena. The twentieth century established vision as a dominant paradigm for studying both sensory information processing and broader brain functions (Shepherd, 2009). However, vision might actually be more of an anomaly than commonly acknowledged.

First take its role as a sensory paradigm: Vision's specific neural organization is intricately tailored to spatial navigation, decoding information from the predictable stimulus of photons. Other senses like touch and olfaction, however, have evolved to respond to unpredictable stimuli, such as airborne volatiles in olfaction, which are influenced by complex fluid dynamics. Unlike vision, most sensory systems handle regularity without predictability, such as interoception (de Vignemont, 2023), which relies on maintaining physiological equilibrium. Exploring the diversity among the senses reveals more than varying evolutionary paths shaped by distinct body-environment interactions, thereby offering a more granular view of neural functionality and its adaptive strategies. It also emphasizes the significance of embracing a 'task-ontology' approach in neuroscience (Burnston, 2021; Nau et al., 2024)—a perspective that sheds light on how differences among sensory systems reveal diverse behavioral adaptations and elucidate the brain's underlying mechanisms for executing these varied functions.

Next consider vision's role as a paradigm for general brain function: The profound influence of vision in shaping the history of neuroscience, becoming closely tied to specific modeling paradigms, may now be to its detriment—especially as the demand for alternative models is growing. To be sure, highlighting alternative systems, such as olfaction, does not imply that no unified causal principle might exist between these systems. Instead, it suggests that alternative systems help us move beyond our current conceptual blind spots, offering fresh perspectives on traditional paradigms. In this context, olfaction emerges as an ideal candidate for such an alternative. Recent discoveries in olfaction, especially representational drift—with the subsequent discovery of similar phenomena in parts of the visual cortex (see footnote 5)—, challenge the traditional view that neural activity patterns remain stable over time. These insights into neural drift suggest a dynamic and non-static nature of brain function, prompting a reevaluation of how we understand sensory, motor, and cognitive processes (Micou and O'Leary, 2023). This dynamic processing exemplified by olfaction, particularly in how it combines external and internal sensory information, positions it as a powerful model for exploring 'embodied' theories of perception and cognition (Chemero, 2011; Crippen and Schulkin, 2020). It highlights the need to shift from models that prioritize static representations to those that accommodate the dynamic nature of neural processes in brain-body-environment interactions. Consequently, while vision has historically served as a foundational model, the evolving understanding of neural plasticity and dynamic information processing—evident in olfaction—underscores the potential of this sensory system to model broader, more generalizable neural mechanisms. Notably, this shift aligns with an increasing twenty-first century focus on neuroplasticity and challenges traditional notions of static neural representations by suggesting, for example, that alternative modeling frameworks such as dynamic systems theory offer valuable new perspectives in neuroscience (Barwich and Severino, 2023). Insights gained from an alternative model system like olfaction thus can either bolster a general model of neural processing or prompt a critical reevaluation of the prevailing theoretical framework or some of its central premises.

The broader issue that we stress in this section thus is the question why vision has dominated brain models for sixty years when olfaction offers an alternative model with its own distinct advantages. These advantages include:

- Topographic mapping vs. nonspatial representation

- Significant circuit processing (especially in the retina) vs. a shallow circuit of two synapses from the world to the cortex
- Continuous, low-dimensional stimuli vs. discrete, high-dimensional stimuli
  Linguistic richness vs. relatively impoverished linguistic descriptions (how do we process sensory information without descriptive language?)[6]
- A stable stimulus world vs. unpredictable novel stimuli, etc.

Beyond these general points that highlight the importance of studying olfaction in the broader context of neuroscience, we now want to conclude with a positive proposal: a concrete alternative to the topographic mapping paradigm.

5. *Application in Scientific Modeling: Transient information patterning and memory encoding without spatial representation*

Here we examine how the genetic underpinnings of the olfactory system offer a fresh perspective on sensory processing that includes molecular mechanisms for dynamic sensory memory encoding. While the genetics of the olfactory system deserve comprehensive study (Keller and Vosshall, 2008), we must limit our focus on genetic transcription (Olender et al., 2016). By realigning our models of sensory signaling to more closely consider genetics—particularly the transcription mechanisms governing stimulus encoding and modulation of neural activity—we may achieve significant conceptual breakthroughs. Ultimately, developing a framework grounded in genetics holds the potential not only to enhance our models of olfaction but also to refine our overall understanding of signal processing in the brain. We begin by integrating recent key findings, exploring how transcription mechanisms are linked to the dynamics of information processing in olfaction. Following this, we offer a conceptual interpretation for sensory encoding models.

5.1 Genetic Transcription: Perceptual Variation and Experience-Dependent Modulation

[6] The view that olfaction is linguistically impoverished is contested; see Majid and Burenhult (2014); for context Barwich (2020a).

Genetic transcription, which regulates gene expression, is crucial for cell functionality, differentiation, and environmental adaptability, offering a unifying perspective on how cellular processes underpin dynamic encoding of environmental information. Over the past 15 years, and particularly in the last decade, transcription mechanisms have gained attention in neuroscience, especially in olfaction research (Ignatieva et al., 2014; Segura et al., 2018). In the brain, transcription mechanisms modulate neural processing, adapt brain functions to new experiences, maintain cognitive functions, and respond to environmental changes. The genetic underpinnings of the olfactory system may explain some of its more perplexing features, including its operational detachment from a topographically organized cortex and the strikingly personal variations in odor perception observed among individuals.

To examine how odor encoding is structured by transcription mechanisms, we highlight three key genetic characteristics of the olfactory system. First, the olfactory system exhibits remarkable heterogeneity, with each person's OSNs expressing a unique set of odor receptors. We point at the genetic diversity of the olfactory system to illustrate how incorporating the genetic features of a sensory system can instruct 'higher-level' models of perception, as this individual expression profile contributes to the diverse ways people perceive odors (Trimmer et al., 2019). Second, the olfactory system demonstrates experience-dependent transcription plasticity, which modulates OSN activity in response to different environments (Tsukahara et al., 2021). This plasticity allows the system to adjust dynamically to new and varying chemical stimuli, enabling adaptive sensory processing and transient sensory memory encoding. Third, different OSN subtypes respond uniquely to sensory experiences, resulting in individualized transcriptional profiles (Tepe et al., 2018). Each neuronal subtype processes and adapts to sensory information in a distinct way, driven by its unique genetic transcription profile. Collectively, this creates a personalized receptor response repertoire in our noses, allowing individuals to perceive their environment in a remarkably tailored way.

First, *genetic heterogeneity*: The human olfactory system is highly heterogeneous and diverse across ethnic populations and individuals (Logan, 2014). The ~400 genes for odor receptors in the olfactory system exhibit significant genomic variation, contributing to unique personal receptor repertoires. Of the variation present, 20-40% of the receptor repertoire is formed by heterozygous haplotypes some of which may be maintained by balancing selection. More

specifically, the genetic foundation of olfactory receptors in both humans and dogs is marked by evolutionary forces such as genetic drift, purifying selection, and balanced selection (Olender et al., 2012). This array of genetic variations in mammalian odor receptor genes contribute to the diverse ways people perceive odors (Keller at al., 2007; Menashe et al., 2007; Lunde et al., 2012; Trimmer et al., 2019).[7] Even a single OR gene change can alter odor perception, with loss-of-function variants often associated with decreased intensity. Due to the large number of non-functional pseudogenes, these variations are crucial contributors to the range of odor perception in a population.

The significance of genetic heterogeneity in olfaction has been overlooked, most likely due to the reliance on genetically homogeneous model organisms like mice and fruit flies. Studies of the human olfactory system show that predictions based on these models do not straightforwardly translate to genetically diverse humans. For example, in model-mice, each olfactory sensory neuron (OSN) expresses one of 1,100 odor receptors (ORs), and OSNs with the same receptor send their axons to about two of the 1,800 glomeruli in the bulb, creating a 2:1 convergence ratio. 'Wild type' humans, however, express around 400 ORs, with over 5,500 glomeruli, resulting in a 16:1 convergence ratio. This divergence suggests that odor coding in humans may involve more glomeruli for a more detailed odor representation (Maresh et al., 2008). While the full implications are still debated, the genetic basis of the olfactory system is crucial for understanding how odors are encoded and perceived.

Second, *experience- and environment-dependent neuronal activity*: Genetic diversity in OR expression is closely linked to individualized transcription networks in OSNs. Each OSN has a unique transcriptome defined by its expressed OR, with distinct clustering based on different ORs (Tepe et al., 2018). For example, OSNs expressing Olfr727 differ from those expressing Olfr728 or Olfr729. This highly specialized gene expression is directly tied to the specific OR each OSN expresses.

These genetic transcription changes yield significant implications for our understanding of sensory encoding models. Tsukahara et al. (2021) demonstrated that OSN transcriptomes

[7] Early investigations into the causal factors influencing individual variability in odor perception, particularly regarding androstenone, were conducted by Wysocki, Dorries, and Beauchamp (1989).

reflect environment-dependent activity (or environmental states, henceforth: ES), which has significant implications for sensory encoding models. They showed that OSN activity adjusts to different chemical environments, with ES scores increasing or decreasing when OSN activity was artificially raised or lowered. In naturalistic odor environments, about 45% of OSN subtypes exhibited significant shifts in ES scores, indicating that specific odors engage distinct ORs differently. Based on these findings, Tsukahara et al. proposed a transcriptional 'rheostat model' where gene expression adjusts sensory responses based on a neuron's history and current activity (figure 6). Using single-cell RNA sequencing (in mice), they revealed that each of the 1,000 OSN subtypes has a unique transcriptome dictated by its OR, enabling unique responses to environmental odors. This diversity allows OSNs to adapt dynamically to changing sensory inputs, with over 70 genes modifying responses based on past exposures and environmental changes.

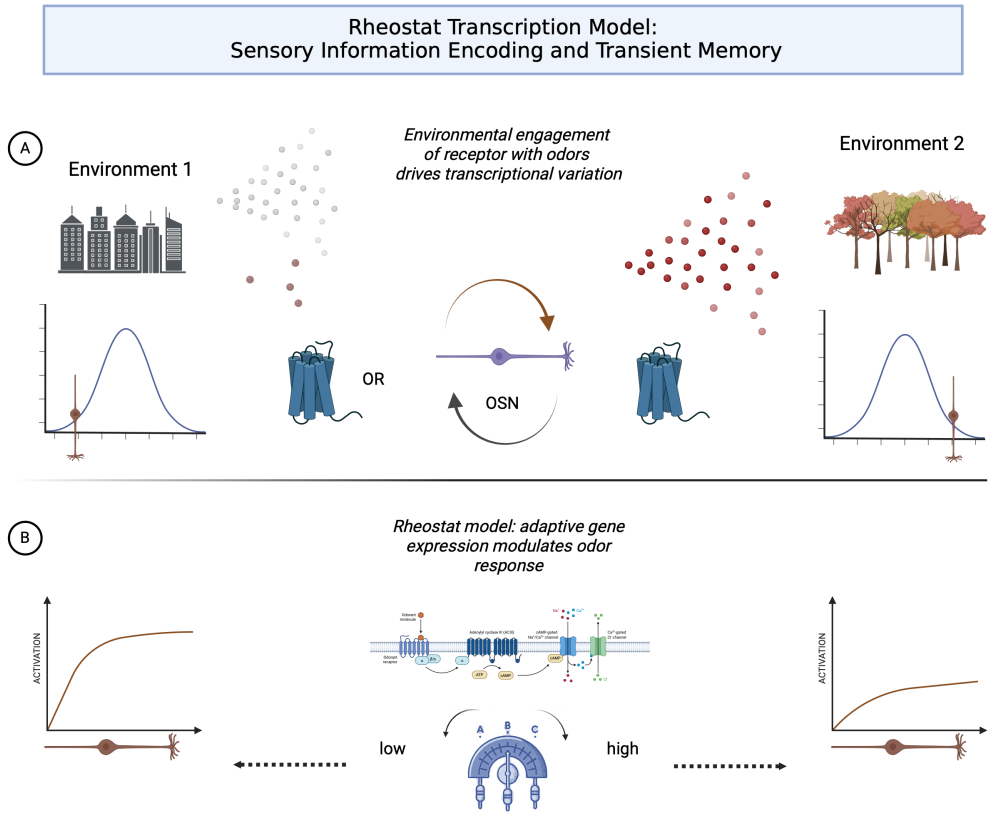

Figure 6 (Barwich, created with BioRender; modelled after Tsukahara et al. 2021): Transcriptional Rheostat Model. *(A) Olfactory sensory neurons possess unique, odorant receptor-specific transcriptomes. Environmental odor engagement drives transcriptional variation, leading to adaptive*

changes in gene expression and odor responses. (B) The rheostat model suggests that adaptive gene expression modulates odor response. In vivo imaging shows that peripheral odor codes vary across environments. Olfactory sensory neurons adaptively shape their responses, distinguishing salient cues from predictable background.

These transcriptional variations are organized and predictable based on OR-environment interactions, aligning with functional changes in odor processing and perception. By regulating genes that convert chemical signals into neuronal spikes, adaptive transcriptional responses in OSNs modify sensory perception, creating a form of transient 'sensory memory' that influences future responses. Environmental changes drive gene expression adjustments in OSNs, preparing them for anticipated stimuli and encoding experiential learning at the cellular level. This supports a broader model where neurons customize their transcriptomes to efficiently handle expected environmental stimuli.

This *experience-dependent genetic transcription plasticity* in the olfactory system differs from the more general experience-dependent developmental plasticity and wiring observed in other senses, such as vision. Sensory neuron activity is modulated through transcription profiles to be environment-dependent, meaning the genetic expression patterns within OSNs are dynamically adjusted based on environmental stimuli. As OSNs encounter different odors, their gene expression changes, tuning the neurons to be more or less sensitive to specific stimuli. This environment-dependent modulation allows for a flexible and adaptive sensory system that can learn from past experiences and anticipate future stimuli, as well as *unlearn* these experiences, providing a form of short-term and flexible sensory memory at the cellular level.

Third, *functional diversification* (at the cellular level): Research on OSN-specific transcriptomes further shows that different neuronal subtypes are uniquely affected by sensory experiences. Genetic expression patterns in OSNs vary with sensory input, such that neurons in enriched environments exhibit different transcriptional changes than those in deprived settings. Each neuronal subtype processes and adapts to sensory information in a distinct way, driven by its individual genetic transcription profile. Thus, transcriptional mechanisms in OSNs significantly influence the functional diversity of neurons in the bulb. For instance, profiling transcriptomes from neurons at various stages of development and under different sensory conditions (naive,

deprived, enriched), Tepe et al. (2018) uncovered developmental pathways and activity-dependent changes in gene expression. These changes impact how neurons respond to new sensory inputs, linking external sensory experiences to internal genetic modifications, and showcasing how external stimuli lead to internal cellular changes governing synaptic remodeling and circuit integration.

In sum, we suggest that these three features—genetic heterogeneity, experience and environment dependent transcription plasticity, and cellular functional diversity—contribute to the olfactory system's two most significant functional capabilities: its ability to recognize and respond to familiar odors and sensory backgrounds, while also being highly adaptive to new chemical environments and changing physicochemical stimulus combinations. In essence, different circumstances elicit varied sensory responses from individuals. The heterogeneous genetic makeup of the olfactory system, combined with its adaptability through OR-specific transcription profiles, provides a versatile and adaptable causal framework for personalized and contextually tailored sensory responsiveness.

5.2 Morphological Computation: Sensory Encoding sans Topography

The role of transcription mechanisms in modulating neural activity is often viewed as an adaptation process. For example, memory encoding activates specific transcription factors like CREB (cAMP response element-binding protein), which facilitate the transcription of genes essential for neuronal functionality and plasticity. This activity-dependent transcription, central to studies of Long-Term Potentiation (LTP) and Long-Term Depression (LTD), ensures that neuronal gene expression aligns with variations in neural activity patterns. In olfaction, transcription mechanisms not only fulfill these general roles but also actively shape how information is encoded at the sensory periphery, particularly in OSNs.

Transcription mechanisms create a dynamic backdrop for information processing, generating a form of transitory peripheral olfactory memory encoding. This ‘short-term memory’ in OSN populations allows them to temporarily imprint aspects of their environment over various time periods, such as seconds, days, and weeks. This record is continuously updated through a

transcriptome-based rheostat adjustment of individual OSN activity. Thus, a significant portion of odor cognition is *offloaded* to computational processing at the periphery via an experience-dependent and environmentally induced short-term memory in odor encoding.

The notion of computational 'offloading' draws from the theories of extended cognition and autonomous robotics.[8] Specifically, morphological computation posits that an organism's or robotic system's physical structure performs 'computational tasks' (Pfeiffer and Bongard, 2006). Applying morphological computation to neural information processing, especially in sensory encoding, involves using the physiological properties of sensory systems for initial processing tasks, thereby reducing energy consumption and minimizing reliance on higher-level processing (Keijzer, 2001; Lyons, 2020). For example, in other sensory systems, the cochlea amplifies certain frequencies due to its shape, and the retina processes visual information such as edge and motion detection within the eye. These offloading mechanisms reduce the computational load for higher-level brain processing, allowing more efficient and rapid responses to environmental changes. In olfaction, the dynamics of genetic transcription mechanisms play a crucial role in offloading sensory information processing.

Transcription mechanisms in olfaction recalibrate the signaling properties of peripheral sensory neurons, reshaping the initial phases of sensory information processing. This improves sensory perception and operational efficiency, which is vital as organisms navigate constantly changing environments. This results in a form of 'transient memory', where OSNs use changes in their signaling activity, driven by environmental stimuli and transcriptional adjustments, to encode and process information over brief intervals. This strategy enables cells to adapt quickly to new conditions, recognize patterns, and reset their states as environmental contexts shift.

[8] In cognitive science, the concept of cognitive offloading challenges the traditional view that cognition is confined to the brain, suggesting instead that cognitive processes extend into the body and environment (Hutchins, 1996; Hendriks-Jansen, 1996; Clark, 2011). This allows tasks like memory or computation to be offloaded onto external media, such as using paper for calculations or microscopes for scientific investigations. We also encounter this concept in autonomous robotics, where robots are engineered to leverage their physical structure to reduce the need for active control and computation (Brooks, 1999; Beer, 2003). For example, robots might utilize specific body shapes to simplify motion control or incorporate soft materials to adapt to various objects without relying on complex sensors.

This experience-dependent, transient sensory memory for contextual encoding matches the ecological characteristics of chemical stimuli. Odorants frequently appear in varying chemical contexts, each altering their behavioral significance and perceptual interpretation. For example, indole in fecal plumes signals 'contaminant,' whereas the same compound in coffee aroma does not carry the same implication.

By focusing on transcription-based activity modulation, it transpires that topographic representation is not essential for pattern recognition in sensory information processing. This suggests that ‘the logic of odor cognition’ need not rely on integrating neuronal signals into spatial activity patterns.

How does this analysis of olfaction extend to other sensory systems and broader neuroscience? These observations invite a reassessment of neural encoding across various sensory systems. The olfactory system’s parallels as well as divergences from vision and other sensory systems highlight the importance of exploring alternative model systems. Such exploration can uncover underlying causal relationships and processes that might otherwise remain hidden.

6 Discussion

This paper critically reevaluated the longstanding topographic model in neuroscience, which traditionally maps the brain as structured three-dimensional spaces reflecting the external world. Despite its historical prevalence, evidence increasingly suggests that not all sensory cortices exhibit a columnar organization, and the definitiveness of neural maps is now questioned. Indeed we argued that rigid adherence to this model has limited our exploration of alternative frameworks, thereby constraining our understanding of neural functions.

It is crucial to recognize that sensory perceptions across different modalities do not necessarily arise from similar causal processes. Unless one assumes that sensory processes share an evolutionary or developmental origin, differences among sensory processes should be expected. Adequate models must map onto both causal processes and their outcomes without

presupposing a unitary model. The marked differences between olfaction and vision, for example, caution against generalizing the topographical model across all sensory modalities. Our analysis of genetic studies of the olfactory system, as well as the recent discovery of 'representational drift' in the piriform cortex, demonstrates that traditional models of sensory encoding, relying on static topographic maps, do not adequately capture the dynamic and flexible nature of sensory information processing.

Extending insights from olfaction to other systems requires accounting for various information processing mechanisms that handle predictable and unpredictable inputs. These systems may or may not share similar genetic underpinnings or operate according to principles like memory and associative learning. Therefore, our central argument for reevaluating sensory processing models emphasizes the importance of exploring alternative mechanisms that have been largely neglected.

Acknowledging causal-mechanistic differences between systems like vision and olfaction does not imply complete disunity in neural processing but rather underscores the importance of deriving principles from the intrinsic characteristics of each system. This paper thus embraced scientific pluralism, not as a barrier to developing a more unified theory of sensory processing, but as a foundational strategy for integrating diverse approaches and model systems. Pluralism is crucial for building a comprehensive theory across different sensory modalities. For example, our exploration of how genetic mechanisms structure information encoding in olfaction aligns with broader rule-based accounts of sensory encoding from studies of the visual system. However, by recognizing the distinct nature of each sensory system, we highlight the limitations of applying system-specific principles universally, potentially mistaking the more idiosyncratic aspects of sensory processing for general principles of neural organization.

Consider two parallels to illustrate a broader shift toward rule-based explanations in scientific models. First, consider the transformation from preformation theory to modern developmental biology (Maienschein, 1997; 2000; 2005). Initially, preformation theory, supported by seventeenth-century scientists like Nicolas Hartsoeker and Antonie van Leeuwenhoek, held that development involved merely enlarging a fully-formed organism pre-existing in the egg or sperm. This view was overturned in the nineteenth and twentieth centuries as discoveries in

cellular biology and embryonic development revealed that development is a dynamic, rule-based process driven by genetic instructions. This shift—from seeing development as predetermined and static to recognizing it as complex and responsive to genetic and environmental interactions—mirrors a similar change in neuroscience. Historically, some views of brain function analogously assumed a centralized 'homunculus' that managed sensory data and decisions (Finger, 2001; Oeser, 2010 [1938]). Meanwhile, modern neuroscience understands the brain as a distributed network where various regions concurrently process inputs, integrate information, and influence outputs, moving away from homuncular interpretations (McClelland, James L., David E. Rumelhart, and PDP Research Group, 1987; Dennett, 1993; Churchland, 1995; Sporns, 2016). Nevertheless, remnants of the homunculus idea persist in contemporary research on the brain's 'wetware', as seen in the topographic paradigm. Our call for a paradigm shift in sensory neuroscience thus reflects a broader transition toward understanding biological processes as rule-governed and adaptable rather than fixed and predetermined.

Another analogy concerns GPS technology, which navigates and processes information through dynamic, rule-based mechanisms rather than static spatial representations. GPS technology dynamically adjusts routes based on real-time data, calculating precise locations using the timing of signals from a network of satellites, rather than relying on fixed spatial maps. This dynamic routing, responsive to current conditions such as traffic and road closures, demonstrates that effective navigation can be achieved through numerical and signal data, processed algorithmically without the need for a visual representation of geographical details. Similarly, in the brain, sensory information processing can operate through dynamic, rule-based mechanisms that adapt to real-time inputs and conditions. Both systems utilize basic sets of instructions to process information dynamically, without a central 'reader' or homunculus, indicating a distributed, rule-based approach to processing tailored to the specific needs and constraints of each system.

These analogies underline the central thesis of our paper: Scientific modeling has progressed from static, deterministic models to dynamic, rule-based models in both biological processes and technological developments. This philosophical and practical transformation in neuroscience proposes that embracing a flexible, rule-based approach to sensory processing

will offer a more precise and adaptable framework for investigating a plurality of neural mechanisms of sensory and cognitive functions.

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