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Measuring the World

Olfaction as a Process Model of Perception

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1. Introduction: Why Things Stink

What is the first thing you do when you open a box of milk, especially if it has stayed a few days longer in the fridge and may have gone off? You take a whiff. Although popular opinion sticks to the idea that the human sense of smell is declining and unimportant, this is a blatant misconception.[1] Your nose actually is the most accurate and sensitive chemosensor on earth. It detects the slightest changes in the chemical composition of your environment, and it does so with striking precision. A difference in one atom of two otherwise perfectly similar molecules can cause your perception of their odour quality to vary entirely. For instance, take nonanoic acid ($CH_3(CH_2)_7COOH$; Figure 17.1a), which smells of cheese. If you add only one carbon atom, you get decanoic acid ($CH_3(CH_2)_8COOH$; Figure 17.1b), which you will perceive distinctly different, as smelling rancid!

While your olfactory system is mind-bogglingly precise in its capacity to detect the slightest changes in chemical variation, it is also incredibly flexible in its processing. Think about the wide range of responses to smells: certain odours evoke an immediate and almost universal dis-liking (e.g., the smell of cadaverine, $NH_2(CH_2)_5NH_2$, is not something you will consider pleasant), but many other odours tend to carry individually variable associations—variable depending on their familiarity and on memories of previous encounters.

This dual character, the flexibility of perceptual interpretation in parallel with the precision of its molecular detection mechanism, makes olfaction an excellent model system for renewing philosophical attention to perception. Perceptual analysis has traditionally concentrated on visual perception. In recent years, the neglect of what is

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[1] The most popular and persistent opinions about our sense of smell are that it is declining, that it is evolutionary unimportant to humans, and that other animals such as dogs are much better at smelling. Nothing could be further from the truth. Neither is the sense of smell declining nor is the human sense of smell considerably worse than the olfactory abilities of dogs. For a popular science account of smell and for debunking such myths, see Gilbert 2008; Shepherd 2012; and Barwich 2016; for a scientific review of the importance of the olfactory system in molecular biology and neuroscience, see Firestein 2001; Shepherd 2004; and Barwich 2015b.

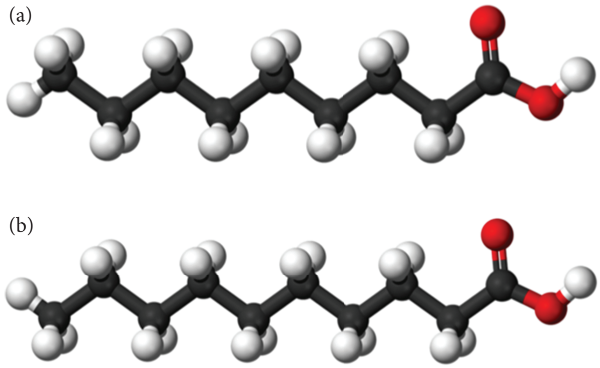

Figure 17.1 Ball-and-stick models of nonanoic acid (A; top), which smells of cheese, and decanoic acid (B; bottom), which smells rancid (Jynto and Mills 2010a, 2010b). While they differ only in one carbon atom, this difference is responsible for their distinctly different smells.

often referred to as 'the other senses' has started to become a matter of correction, though.[2] Nonetheless, olfaction remains the most neglected sense among these laudable developments.

Smell has long constituted the problem child for philosophers of perception because of its apparent lack of representational capacities. Odours are experienced, but in what way does this constitute representational content? This question has been traditionally addressed by debating the representational nature of odours as corresponding to objects (see the essays in the thematic issue of Keller and Young 2014). Such approach centres on the nature of the stimulus as defining perceptual content. In light of recent developments in cognitive neuroscience, I propose an alternative to that view in this chapter.

Perception here is analysed as a *process*. The thrust of my argument is, in brief, that we need to abandon a stimulus-centred point of view where we think of smells as stable percepts that are computationally linked to external objects such as odorous molecules. There are no stable and intrinsic links between chemicals or input sources and our perceptions, such as of odour qualities. Denying that input sources are the primary element in perceptual analysis does not lead to a denial of their causal and functional significance, however. Once this proposition is clear, a very large part of the philosophical motivation to oppose the perceptual model advanced here should vanish. Instead, we must consider flexible and contextual aspects of the process to understand what it is that we perceive from odorous molecules through our sense of smell.

Smells, the argument proceeds, are not so much about objects and stable object perception as about changes in the chemical composition of the environment and flexibility in terms of its contextual evaluation. In the course of percept formation, sensory input is filtered and structured by different anticipatory processes. What we perceive is highly dependent on a signal's combination with other sensory cues, previous experiences, and expectations of what options a signal affords.

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[2] For reviews, see audition (O'Callaghan 2014), touch (Fulkerson 2015), taste and flavour (Smith 2012; Spence 2013).

The informational content of smell must not be analysed as perceptual instances in terms of classes of ‘odour objects’ (e.g. rose), but with respect to ‘odour situations’ where input cues are integrated in terms of their temporal and contextual associations with other external sensory cues, internal hidden states (experience and memory-based, or internally inferred), expectations or predictions, and feedback processes of error correction. A number of processes can cause certain odour qualities to become more prominent in a percept, allowing for semantic associations with previously encountered smells. Other processes facilitate the variability of semantic associations in smell perception. In order to understand the informational content and identify the perceptual dimensions in olfaction we must model odours after the processes that facilitate signal pattern separation and completion.

In this chapter I elaborate on the scientific foundations and philosophical implications of this idea. That said, the perspective on perception advanced in what follows is not meant to carve out olfaction as necessarily different from the visual or auditory systems. Rather, it is intended to refine our perspective on the variable factors that determine perceptual content. Olfaction in this context bears interest, as it seems to possess a less intuitive perceptual structure than vision and, as a result, a less deceptively straightforward relation between sensory input and perceptual content.

The starting point of this chapter is to engage with the received view in philosophical studies that considers the distal stimulus as the central element for the analysis of perceptual content (Lycan 2000; Batty 2010a, 2912b, 2013; Keller and Young 2014; Keller 2016). Having outlined what constitutes the general challenge here, namely the inadequacy of talk about odour objects, I turn to current scientific studies on the neural basis of olfaction. These studies highlight the non-linearity of stimulus processing and demonstrate the impact of top-down mechanisms in olfaction, and I analyse these experimental developments in the context of an alternative framework as emerging in cognitive neuroscience. The central proposal here is to model the brain in terms of two complementary and simultaneous processes as the integrated proximal stimulus: perceptual bias as anticipation and bias correction as revision. I conclude with a disambiguation of the different meanings of anticipatory processes that regulate perception; and I present perception as a process that measures changing signal ratios in the environment and is shaped by expectancy effects in perceptual content formation.

2. The Received View: The Input Determines the Perceptual Experience

In some ways the philosophical analysis of perception used to suffer from the same problems as certain parts of theoretical physics: concepts originate purely from theory, and there often is no way to see how foolproof the grounds for the relevant theoretical convictions really are without guided experimental manipulation. Contemporary philosophy of perception has experienced a great deal of change and challenges in parallel with the rise of cognitive neuroscience over the past decade, however. The essential tension surrounds the double understanding and analysis of perception (1) as a representation of external objects (distal stimulus) and (2) as a result of the neural processes generating stimulus patterns (proximal stimulus).

Take the common-sense idea that our perceptions are shaped by what we perceive: we consider our perceptions to be representations of objects and their features in the world. Philosophers of perception have been careful not to confound perceptual representation with neural representation, and instead have focused on the distal stimulus input as the measure by which we must judge the content of our perceptions. What are the grounds for this view, and what reason is there to reconsider the relation between perceptual and neural representation?

Let's start with the traditional philosophical notion of a 'percept'. Although there seems to be no formal definition of what a percept is, it is commonly used to refer to the perceptual experience that results from the act of perceiving. Our percepts are considered to be *about* things in the world, and understanding this aboutness or intentionality of perception is one of the major occupations in philosophical discourse (Peacocke 2008). For example, my perception of the cup of coffee in front of me is going to tell me something about it, such as its colour, shape, and size. But how shall we model and analyse the content of our perceptual attention to the world?

The philosophical literature has produced numerous arguments on this topic (for a review, see Crane and French 2016). Large parts of the debate concern whether such perceptual experiences are truthful or *accurate* representations of the things we perceive in the world (Akins 1996). Central to this inquiry is the distinction between perceptual appearance and reality. What unites the bulk of philosophical arguments on this topic is a concern about the source of perception and its elemental primacy for perceptual analysis. The shared hypothesis about the directionality of the perceptual process is clear: *the input structures the perceptual content*. What does that mean? And does this apply to olfaction?

The common-sense idea that perception is about objects originates from our dominantly 'visuocentric' theories. It has led some philosophers of mind to the question of what might constitute 'odour objects'. Four suggestions are offered in the literature: (i) smells represent ordinary objects (like roses, wine, or Brussels sprouts); (ii) smells represent clouds of odorous molecules; (iii) smells represent chemical features of molecules; or (iv) smells may be purely subjective phenomenological experiences or sensations that do not present us with propositions specifying particular objects in the world (for different positions, see Lycan 2000; Batty 2010a, 2010b; Keller and Young 2014). Analysis here centres on the assessment of perceptual 'object failure', meaning 'the failure of an experience to present objects accurately' (or to present any objects at all; see Batty 2010b: 10).[3]

A lot of arguments in this debate concern the effect of the visual presence of a source object on olfactory experience (particularly in the work of Lycan and Batty). Notably, this effect has been characterized by the olfactory physiologist Hans Henning as early as in 1916. Henning drew a conceptual distinction between 'the true odor [*Gegebenheitsgeruch*], which is obtained by the observer who is smelling with closed eyes and is ignorant of the nature of the scent, and the object smell [*Gegenstandsgeruch*], which (like color) is projected upon the objects from which it is

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[3] Alternatively, a discussion about the question of whether we can perceive absences in olfaction as being objectless can be found in Roberts 2015.

known to come and apt to be distorted by associative supplementing' (Henning in Gamble's translation, in Gamble 1921: 292). Eleanor Gamble's translation of the German *Gegebenheitsgeruch* as 'the true odor' is misleading, however, as the literal meaning is 'the situation odour'. For Henning, such perceptual effects presented important methodological factors for psychophysical measurement, not a measure of the 'truthfulness' of odour objects.

There are several philosophical difficulties involved in defining olfactory objecthood (for an extensive analysis, see Keller 2016). Some of the arguments about the nature of odour objects, namely for their being (ii) clouds of molecules or (iii) particular features of molecules, fail to distinguish between the stimulus as the *cause* of perception and the perceptual object as the *content* of perception. This view also runs into scientific problems. To date, there are no known structure–odour relationship rules (i.e. regularities linking specific chemical features and the smell of a molecule), and the causal features of odorants (i.e. the odorous molecules) are dependent on receptor behaviour, not vice versa (Barwich 2015a, 2015b; Poivet et al. 2016). Moreover, and as I explain in the next section, smell is not only determined by molecule–receptor interactions, but is also significantly dependent on higher-level brain processes.

Arguments for (i) (i.e. a semantic understanding of odour objects as ordinary objects) run into trouble as well. Suffice it to say that some smells, such as artistic perfumes, do not necessarily have associations with ordinary objects. Even ordinary objects give off hundreds of odorants, and each one is not only different from the others but also distributed from its source at a different temporal scale from theirs (this is also the basic principle in the composition of alcohol-based perfumes).

A layered account for odour objects as being a combination of semantic (= (i)) and causal (= (ii), (iii)) objecthood does not present an intuitive or clear criterion for an odour object either. 'Layered' means, according to Lycan (2014), that odour perceptions can be veridical in two independent ways: first, on a lower-level account of representation in terms of its causal objects (i.e. I perceive, correctly, the presence of a cloud of molecules as the causal object); and, second, on a higher-level account of representation in terms of its semantic associations (i.e. I perceive, correctly, a cloud of molecules as a rose). Such a model of differentiating the truth values of (i) and (ii), (iii) remains far too uninformative and further runs into trouble once we consider the different variables regarding the distal stimulus as well as its associated semantic content. For example, the attempt to link the smell of ordinary objects such as roses to particular (clouds of) molecules (or their features) is

> [a]n innocent approach when we know that the scent of a rose comprises hundreds of different molecules and that none of them smells like a rose. So far I have not found 'the' rose molecule, but I have discovered that the smells of flowers have a biologically dictated cycle, and that their composition can vary significantly without them losing their identity.
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> (Ellena 2012: Cabris, Thursday 22 July 2010)[4]

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[4] To be sure, the basic rose smell is more likely composed of dozens, not hundreds, of molecules. The main point of this statement remains valid, however.

A dominant focus on veridical object representation in perceptual analysis further falls short of several key aspects of olfactory experience. First, it ignores the purpose of smelling: 'Stimulus representation isn't the primary business of olfaction. Rather, its job is solving a problem of valuation, rapidly encoding the biological salience of a stimulus and priming our multisensory representation of it to contextually appropriate action' (Castro and Seeley 2014: 1). As other philosophers and scientists have pointed out (Burge 2010; Keller 2016), the biological function of perception is prior to representational accuracy in an evolutionary reading of sensory systems. Perceptions here are primarily understood to facilitate the achievement of *organismal goals* such as the four Fs (fighting, fleeing, feeding, and courtship). While the truthful representation of the world can coincide with the achievement of these biological functions, it need not.

Second, object-centred representational analysis remains indeterminate and misleading with respect to the perceptual dimensions and the structure of olfactory experience.[5] What is the structure of odour perceptions? To be sure, olfactory information is spatially and temporarily structured in the environment. In humans and other animals it can be used for navigation and active exploration (Porter et al. 2007), and we recognize temporal patterns of changes in the olfactory environment on shorter and longer scales, such as circadian and annual fluctuations of smells (Keller 2016). That said, we must be careful not to equate the external structure of a signal with the structure of our perceptual experience.

Human olfaction is generally characterized as being temporal but as lacking spatial dimensions in its perceptual content. It is temporal in a phenomenological sense, as smells appear to be perceived *now*, and they act as an indicator of the presence of something. Olfaction is also temporal, in the sense that we perceive important changes in the chemical constitution of our environment. As we are constantly surrounded by hundreds of airborne molecules, our olfactory system is tuned to this situation by quickly adapting to stable ratios of odorants, so that neural populations fire more actively when novel stimuli are encountered. In comparison, spatial structure in perception is characterized as exhibiting perceptual relations in terms of position, orientation, or directness (Keller 2016). As odours do not exhibit such spatial structuring and 'we do far less of that sort of objectification' in olfaction, this has led some philosophers to believe that 'smell, in humans, is informationally very poor' (Lycan 2000: 277) and lacks 'articulate individuation' (Lycan 2000: 282).

Such a judgement conveys a blatant misunderstanding of what olfaction is *for*. Information is an ambiguous and multifaceted notion, especially with respect to organisms and their sensory systems. I ask you instead, *how many* different smells can you perceive? Scientifically speaking, olfactory quality space is multiscaled and consists of hundreds or thousands of different odours (though the precise number and the usefulness of counting are matters of debate; see Bushdid et al. 2014; Meister 2015; and Magnasco et al. 2015). Furthermore, why do you consider an odour to be pleasant or unpleasant (and when or for how long)? It is rather

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[5] I have argued in more detail elsewhere why I consider object-centred representational analyses of smells to be ill informed with regard to categories of sensory measurement (Barwich 2014).

curious how much the hedonic tone of odours seems to escape philosophical ideas about perception; one might blame this on the heritage of the Enlightenment's mirthless philosophy of the senses (Classen et al. 1994). Likewise, how much does the context of your encounter with a stimulus and its combination with other sensory cues shape its perceptual content? The most obvious example of the informational richness and context-sensitivity in olfactory perception is the complexity of flavours (Shepherd 2012, Smith 2012, Spence 2013). Your perception of food and beverage flavour is dominated by your sense of smell, more specifically retro-nasal (or mouth-breathing) olfaction. Humans have developed highly sophisticated discriminatory abilities when it comes to flavours.

Overall, such a differentiated account of perceptual information invites us to rethink our standard approach to perception. Regarding the inadequacy of talk about odour objects, other philosophers have suggested adopting suggestion (iv) and simply rejecting an object-representational account, viewing smells as subjective phenomenological experiences or as 'feels' that are somewhat 'free-floating' or 'objectless' (Batty 2010a, 2010b). It remains unclear what precise understanding of odours is gained through this proposal, however. Detaching philosophical analysis of smell from objects and seeing perceptions as mere sensations does not account for the purpose of odour perception as a measure of chemical changes in your environment. It does not explain how we should understand the role of the stimulus as an informational signal for a specific sensory system. Thus this chapter advocates that the structure of the perceptual image must be modelled after the processes it serves. But what are these processes? And how can we think about the informational dimensions of signals in terms of sensory systems and their regulatory principles?

3. The Neural Basis of Olfaction and the Idea of Forecasting in Perception

Input-centred modelling of the senses has not been restricted to philosophical debate. Its equivalent in neuroscience is the view that the organization of a sensory system such as the visual or the auditory one is shaped primarily by the incoming signal. Basically, this expresses the idea that external stimuli are recognized by our sensory systems and translated into internal representations by means of topographically organized brain activation patterns that further facilitate behavioural responses to certain stimuli. The resulting input–output model of perception has been crucial for successful developments in visual research, especially throughout the 1980s and 1990s (Marr 2010 [1982]), as well as influencing research on other sensory systems such as olfaction (Davis and Eichenbaum 1992).

Meanwhile this standard bottom-up version of computationalism has been challenged and modified.[6] Over the past decade, sensory and computational neuroscience

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[6] The implicitly unidirectional and monocausal input-to-output interpretation of sensory processing has elicited various criticisms and suggested alternatives over the years, especially in philosophy. Most prominently, theories of action, enactivism, and embodiment have argued against the differentiation between perception, body, and the environment (for an extensive review, see Hurley 2001). Overall, these theories view the body as a condition and constraint for forming percepts so that we are able to

has provided much more advanced models and analysis of higher-level brain processing. While we should not equate the analysis of the sensory processes with the phenomenological character of its perceptual products per se, the neural pathways are the basis on which we must build and correct our perceptual theories. What is more, by identifying and analysing current questions in contemporary neuroscience, we gain a much more detailed and informative picture of what kinds of questions we must ask in order to reconsider some philosophical approaches to perception. Olfaction, again, presents us with a salient case for this.

As a rough sketch (see Figure 17.2), the olfactory pathway is structured as follows (for a review, see Firestein 2001). Odorants are first detected by receptors situated on the sensory nerves in the nasal epithelium. All olfactory sensory neurons expressing one particular receptor gene (encoding a receptor type) are then collected in spherical

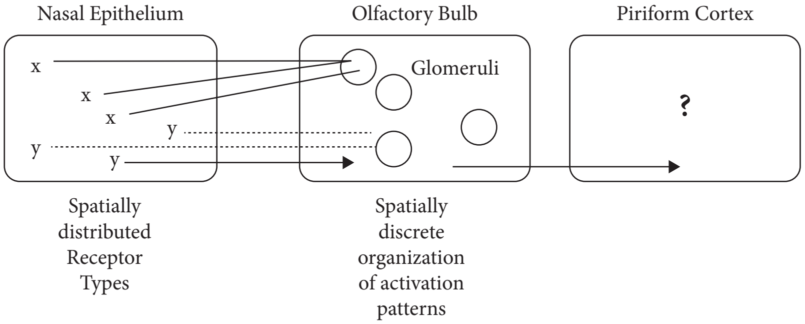

Figure 17.2 Sketch of information flow in the olfactory pathway. Odorants activate receptors situated on the sensory nerves in the nasal epithelium. Receptors are randomly spatially distributed across the mucous. All sensory nerves expressing one receptor gene (coding for a type) are collected in neural spherical structures called glomeruli. As a result, odors here are represented as spatially discrete activation patterns. The synaptic organization of the piriform cortex remains an unresolved issue to date.

interact with our environment through sensory experiences. Or, more briefly put, the state of your body affects the state of your perception and, in turn, of your cognition. On this account, behavioural or motor output and sensory input are coupled and analysed in relation to each other (Varela et al. 1991; Hurley 1998; O'Regan and Noë 2001; and Noë 2004). I have decided to exclude analysis of embodiment ideas in this chapter, for reasons not only of length and focus, but also of appropriateness: strong theories of embodiment that view perception as being somewhat in the body and *out of our heads* (Noë 2009) simply fail to resonate with numerous clinical cases, for example where certain disorders in the right-brain hemisphere can cause feelings of disembodiment in patients (see ch. 3 in Sacks 1998). However, I agree with weaker theories of embodiment that emphasize sensorimotor aspects of sensory systems as influencing perception (e.g. the effects of sniffing patterns on odour perception). One can be of a divided opinion as to whether sensorimotor effects require such an extensive theoretical treatment as in the case of the embodiment movement. In fact some psychologists have objected that the 'basic principles from embodiment theory are either unacceptably vague (e.g., the premise that perception is influenced by the body) or they offer nothing new (e.g., cognition evolved to optimize survival, emotions affect cognition, perception–action couplings are important)' (Goldinger et al. 2016: 959). I remain agnostic on this issue in this chapter.

neural structures (so-called glomeruli) in the olfactory bulb (at the frontal lobe of your brain). At the bulb level, a neat activation pattern shows up (Vassar et al. 1994; Mombaerts et al. 1996). This pattern represents the range of receptors that are activated by certain chemical features of the distal stimulus. So you will get a different activation pattern for a musk molecule from the one you will get for a citrus molecule. Now, as with the visual system, this topographic organization of the bulb was expected to be maintained throughout further processing stages, and the expectation was to find a corresponding topography in the olfactory cortex (Axel 2005). It turns out that this may not be the case.

Olfactory scientists have struggled to find any such topographic organization over the past ten years (Stettler and Axel 2009; Mori et al. 2006). Their efforts have largely concentrated on the so-called piriform cortex, which constitutes the largest part of the olfactory cortex. It was long assumed to be the centre of odour object formation. This means that the piriform was considered to be the domain in the brain where olfactory signals are combined into a unified odour percept. While the piriform cortex does not present us with stable input maps like the bulb, it has been shown to respond to different sorts of organizational regulation, however.

On the one hand, there are findings that suggest that the piriform cortex can get trained into forming more or less temporally stable patterns through innate as well as through learned behaviour (associated with smells). This strategy is pursued for instance in Richard Axel's lab. Taking full advantage of the experimental possibilities offered by novel techniques such as optogenetics, Axel's team traces olfactory signalling from the bulb to the piriform cortex via the amygdala as a sort of 'relay' station (Root et al. 2014). The amygdala is part of the limbic system and deeply involved in processes of memory formation, decision-making, and affective responses.

On the other hand, an alternative model is to 'reverse engineer' and ask what the signal is *for* (i.e. trace its efferent connections) rather than ask where it comes from (i.e. trace its afferent connections). This strategy is employed by Stuart Firestein's lab. Firestein's team was looking at projections from two higher-level domains in the orbitofrontal cortex (the agranular insula and the lateral orbitofrontal cortex) back to the piriform cortex. And indeed, the team found two distinct neural populations with a largely non-overlapping topographic organization (Chen et al. 2014).

To what extent these findings will converge in a unified model of olfactory processing is an empirical question, and it presents an exciting prospect for further research in olfaction. There may or may not be a central domain of synthesizing or unifying olfactory experience. What these approaches have in common thus far is a shared focus on behaviour and learning as fundamental to the formation of odour objects. The amygdala and the orbitofrontal cortex in particular are domains notable for their involvement and centrality in decision-making processes and sensory integration (Shadlen and Kiani 2013; Castro and Seeley 2014).

For philosophical studies of perception, these are interesting experimental developments. They highlight the non-linearity of stimulus activation and representation and demonstrate the impact of top-down neural processing in olfaction. While research on smell lacks a general theory of its subsystems (integrating studies of receptor, bulb, and cortex activity), these experimental inquiries resonate with a general tendency in cognitive neuroscience that has started to pursue an alternative framework for modelling perception and cognition. The growing trend is to think of behavioural systems in computational terms.

While there is no real consensus about theories of the brain to date, there is convergence on what aspects a genuinely alternative conceptual framework for neural processing must build on: bias and revision. 'Bias' refers to the formation of anticipations and preferences through previous experiences, and revisions are processes where these biases are continuously corrected.

Consider a great example of perceptual biases introduced by top-down processing: the role of expectations in flavour perception. Here we encounter numerous phenomena where the perception of colour or texture in foods and beverages affects our judgement about the perceived gustatory qualities of these foods and beverages. In one study, test subjects were given two beverages of the same chemical composition, one being of a brighter colour than the other. Subjects perceived the brighter beverage as sweeter and more intense (Bayarri et al. 2001). Another study appears to ridicule sommeliers and wine tasters who were given wines to test and describe. The subjects in this study were presented with red wines that, unbeknownst to them, were in fact just white wines laced with red food colour. The tasters proceeded to attribute traditional red wine properties to these white wines (Hodgson 2008).

What perceptual puzzles such as these suggest is that seemingly higher-level processes should not be taken as separable modules in the cognitive architecture. They are an integral part of our basic perceptual processing instead. As has become clear by now, perception is not exclusively or even primarily determined by input. Most notably, this is where data from the neural pathway and psychophysical studies of perception converge. What we perceive with the help of our sensory systems is multilayered and multiprocessual: perception is dependent on a signal's combination with other sensory cues, previous experiences, and expectations about the kinds of options this signal affords. These different processual layers are constitutive of the perceptual architecture and the selective biases in percept formation. But how can we model and analyse such seemingly bidirectional causal character of information flow in sensory processing?

Over the past fifty years, a number of neuroscientists have suggested models of neural networks that build on these two processes, anticipation and revision, as complementary mechanisms. In these models, your brain works like a neurocomputer that copes with the plethora of sensory information by predicting stimulus regularities through previous experiences. These sensory regularities provide perceptual templates by which your brain continuously generates an internal virtual model or a simulation of the environment (Friston 2010; Graziano 2013).

To generate such a model, the brain operates by two complementary and simultaneous mechanisms of top-down and bottom-up processing. 'Top-down processing' refers to the information flow from the higher cortical areas to the lower sensory domains. This top-down mechanism makes predictions about the environment on the basis of prior experience of stimulus regularities, and its activity results in so-called 'forward models'. By comparison, bottom-up processing describes the information flow of stimulus input from lower sensory areas to higher-level brain domains. Most crucially, the function of the incoming input from this bottom-up mechanism is defined as an error correction of the forward model. What precisely such top-down processes are and what constitutes the content of predictions is not obvious, as I will explain over the course of what follows.

Similar models of the brain as a perceptual forecasting machine have permeated motor theories for decades (Bridgeman 1995, 2013). For example, one of the most salient examples for the role of sensorimotor prediction in perception is a phenomenon that was first described in the nineteenth century (Bell 1974 [1823]; Purkinje 1825; Helmholtz 1925 [1866]) and later, in the mid-twentieth century, became known as 'efference copy' (Holst and Mittelstaedt 1950; Sperry 1950). Efference copy describes an effect where your brain creates a forward copy of your sensorimotor system, anticipating your movement in order to provide stability in motion perception (Bridgeman 2007).

More recently, the idea of the brain as a forecasting processor has entered cognitive neuroscience and philosophy under labels such as the theory of predictive coding, or the Bayesian brain (Friston 2010; Clark 2013; Hohwy 2013), but also as attention schema theory (Graziano 2013). The essential components for such theories have been around for several decades and in various disciplines. The importance of schemata as perceptual anticipations in perceptual cycles and revision was put forward most prominently by the cognitive psychologist Ulric Neisser (1976), a close colleague and office neighbour of James J. Gibson at Cornell.

While the various subtleties and differences in different theoretical accounts of forecasting mechanisms need not concern us here, what essentially unifies these approaches, in my view, is a shared outlook on the nature of perception and cognition as inherently processual. In forecasting models, perceptual analysis is not centred on the idea of stable piecemeal perceptual images of the world as representative of external objects. Rather, it concerns the dynamics between anticipation and correction in perception, and the processes that constitute the formative mechanisms of learning and revision. Such a dynamic picture accounts for the flexibility with which organisms are able to react to a variety of environmental changes.

In this perspective, the links between input and output processing are deeply intertwined and cyclical. Their analytic differentiation is not so much of a sequential as of a functionally complementary nature. Therefore the first step here is to acknowledge the central difference from the received view, where we saw the perceptual images as a product at the end of the line of the perceptual mechanism. The flaw of the received view is that it obscures the constant flux that directs perceptual processes. Or, in Dennett's (1993: 253) words: '[t]his is like forgetting that the end product of apple trees is not apples—it's more apple trees.' This, too, holds true for perceptual analysis if we are forgetting that the end product of perception is not percepts—it is the ongoing perceptual processing.

When we analyse perceptions in terms of such forecasting processes, our perceptual images are not shaped exclusively by the external input but are strongly affected by our anticipations, experiences, and the information context. Anticipatory processes are not some isolated effects at the end of higher-level cognitive processing. Rather, they resonate with neural mechanisms that constantly feed back into lower sensory domains and thereby influence the biochemical effects that produce our perceptual impressions. That said, discarding the primacy of input as structuring our perceptual experience does not mean that the stimulus does not play any role at all, only that its role must be modelled after the processes in which it participates.

It is one thing to say that the formation of percepts is informed by signal input but shaped by top-down processing. It is another to highlight the concrete aspects of top-down processing that benefit our understanding of perception as processes. To put some flesh on the bones of this idea, I present the case of an alleged 'olfactory illusion' in the next section, before ending with the concrete philosophical questions that result from a perceptual model based on processes instead of objects. Ambiguous meanings of anticipation are the easiest place where we can situate prospective work for philosophers of perception—work complementary to current developments in cognitive neuroscience.

4. The Interactivity of Forecasting and Stimulus Input in Perception

The picture of the general framework sketched above is permissive and allows for several levels of description in perceptual analysis with respect to the neural and mental processes. In essence, the perceptual architecture we arrive at here is a relational and temporally scaffolded one: perceptual relations are built over several neural processing levels and temporal scales, where some anatomical, physiological, and experiential constituents of the perceptual process are more variable, contextual, or short-lived than others (e.g. exposure time to stimulus, satiety, hormonal states, anatomical features). Stimuli are encountered in manifold organismal states and in various behavioural and environmental contexts. In consequence, they are processed differently as they become integrated into multiple experiences and memories, and can constitute varying perceptions. The complex role of anticipatory processes in the formation of perceptual content cannot be underestimated. An example may help to further illustrate this.

Imagine the following experiment, where I present you with a couple of odorous mixtures for evaluation. First I am giving you a vial to sniff that you see labelled as 'Parmesan'; then I give you one labelled as 'vomit'. You will most likely be able to distinguish these mixtures; and you will probably find the latter much more disagreeable. I then repeat the same test a week later, only this time making you smell the 'vomit' vial first and giving you the one with 'parmesan' next. You will still be able to tell them apart, finding the former more unpleasant this time. What if I tell you now that these two vials are the same mixture? Both vials contain butyric acid ($CH_3CH_2CH_2$-COOH) with its deeply unpleasant and penetrant odour. Your expectations and the associations formed through the labels, however, influenced your perception of these otherwise chemically equivalent mixtures.[7]

Indeed, such an experiment, analysing the 'influence of verbal labeling on the perception of odors' (as the title of the article indicates), has been conducted, for instance, by Herz and von Clef (2001). In this study the two researchers tested several odours by pairing, for evaluation, two vials with mixtures of the same chemical composition but with different names (Table 17.1). The result was precisely the one described above: the vast majority of human test subjects (83 per cent) were able to distinguish the mixtures in each round and attributed different hedonic tones (pleasant or unpleasant) to these mixtures. Similar observations have also been

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[7] Theories of embodiment do not seem to provide a good explanation for such cases.

Table 17.1. Odour labels and hedonic order by group and session. Comparative list of odourous mixtures that were presented to test subjects under two different labels. The evaluation of the hedonic tone (pleasantness) of the mixtures corresponded with the positive or negative semantic labelling of these mixtures.

Odorant	Label, session 1	Label, session 2	Hedonic order
Group 1			
I – B acid	parmesan cheese	vomit	positive, negative
Menthol	chest medicine	breath mint	negative, positive
Patchouli	musty basement	incense	negative, positive
Violet leaf	fresh cucumber	mildew	positive, negative
Pine oil	spray disinfectant	Christmas tree	negative, positive
Group 2			
I – B acid	vomit	parmesan cheese	negative, positive
Menthol	breath mint	chest medicine	positive, negative
Patchouli	incense	musty basement	negative, positive
Violet leaf	mildew	fresh cucumber	positive, negative
Pine oil	Christmas tree	spray disinfectant	positive, negative

Source: Herz and von Clef 2001

made regarding the influence of visual clues in olfactory perception (Zellner and Kautz 1990).

Herz and von Clef call this effect an olfactory ‘illusion’. While it may count as one according to the received view, I find this kind of labelling of perceptual effects theory-laden and misleading. The judgement or verdict that something is an illusion conveys an inherent element of deception and divergence from how things ‘really’ are. To speak of an illusion in this particular experiment seems intuitive only if we consider the distal stimulus as primarily responsible for the content of our perceptions. However, the argument of the present chapter shows that this is not the only viable interpretation of the apparently illusionary effects. Quite to the contrary, such perceptual biases touch base on what perceptions *are*.

Examples like these show that our experience of perceptual qualities is inevitably biased. These biases are not necessarily a matter of illusion, hallucination, or deception and must not be stripped away in order to get at some underlying form of normal and unbiased perception. In fact, there is no such thing as naïve perception. Perceptual biases are rather introduced by key factors such as exposure, predilections, and memory. Hence biases mark constitutive processes that allow us to understand what perception really is about: the processing of contextualized information at the hands of selective attention.

In recognizing the impact of top-down processes on percept formation, an insufficiently elaborated aspect in the current debate about the brain as a forecasting machine is the ambiguous meanings and varieties of top-down processes such as anticipations.[8] As a general term, anticipation refers to the ability of an organism to expect, adapt, and react to potential future states of the environment. Anticipation is not a homogeneous mechanism, however. It is a processing capacity that is commonly associated with a variety of fundamental cognitive mechanisms such as inference- and decision-making, prediction, learning, memory, and belief formation (Butz, Sigaud, and Gérard 2003). Needless to say, each of these processes presents a case of Pandora's box in its own right.

While anticipatory performances in organisms are ubiquitous, they are not particularly well-understood phenomena. They are generally considered in systems-biological terms, for instance an organism as an anticipatory system is defined as 'a system containing a predictive model of itself and/or of its environment, which allows it to change state at an instant in accord with the model's predictions pertaining to a later instant' (Rosen 2012: 399).

What current forecasting models in computational neuroscience focus on is the first part of this definition, namely the part where the system generates a predictive model of the stimulus environment (Clark 2013). But the second part, where the *organism changes state in accordance with its anticipations*, requires more careful attention than is presently given. By focusing on the former, one essentially neglects (a) the phenomenological and functional nature of perceptions as an incentive for organismal agency; and (b) the ecological relation between perceivers and input signals as part of an organism's environment.

Indeed, there is a fascinating aspect to this definition of organisms as anticipatory systems. Its two parts seem to represent a combination of Neisser's (1976) dynamic account of schemata as part of perceptual cycles with the ecological and exploration-oriented theory of affordances advanced by his colleague Gibson (1966), who considered the content of perceptions as structured by the interactive relations that an organism forms with its environment.[9] It seems that a dynamic modelling of said schemata in terms of different kinds of anticipatory processes may work here, as Neisser characterized the causal nature of dynamic anticipatory schemata on perceptions as 'expectancy effects' (Neisser 1976: 43–6).[10]

Anticipatory capacities in organisms clearly structure behavioural and cognitive patterns. They further seem to facilitate various kinds of perceptual tasks, tasks that

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[8] As has been pointed out to me by a reviewer, a process model of perception involving anticipation has been independently suggested by Bickhard (2009). Bickhard frames representations as an emergent feature of perceptual systems and as a result of interactive relations between an organism and its environment. Bickhard's focus is on the relation between anticipation and truth values for the representational analysis of perception. Mine is on the role of anticipation in affecting perceptual content for understanding and modelling the structure of perceptions, especially in olfaction. Unlike me, Bickhard does not seem to distinguish different kinds of anticipatory processes as defined by their ecological and action-(in)dependent functions.

[9] To be sure, Gibson was clearly opposed to schemata, and his idea of 'direct perception' seems to be at odds here. Nonetheless, one must refrain from a simplistic interpretation of direct realism as a form of the 'textbook Gibson' syndrome (for detailed analysis of how much Gibson's ideas have been misrepresented in the psychological literature, see Costall and Morris 2015).

[10] I thank Ingvar Johansson for pointing this out to me. A more detailed exploration of this idea must wait for another occasion, however.

are mirrored in organismal behaviour such as general object and environmental feature recognition, or the recognition of particular individuals and groups. It is thus indispensable to distinguish different types of anticipatory processes in relation to different behavioural patterns and perceptual tasks in organisms.

What are the implications of anticipatory processes for our analysis of perception? The answer to this lies in inquiries about what precisely is coded or estimated in top-down anticipatory processes and how these anticipations are structured by the task a perception is supposed to serve. Anticipatory performances are associated with several prospective mechanisms such as sensorimotor action, expectation, and attention processing with and behavioural functions such as conditioning and learning. These mechanisms are associated with different tasks. When looking at anticipations as shaped by different biological mechanisms, we must start by distinguishing their perceptual function: do we look at anticipations as *stabilizing* perceptual information in order to allow for the execution of an action? Do we analyse anticipations as *guiding* behavioural planning and potential options? Or do we model anticipations as attention processes that *shape* or *direct* our perceptual focus in order to enable learning?

Addressing such questions requires further disentangling of the notion of ‘anticipation’ and of its role in perceptual processing: physiologically speaking, we must consider to what extent action-dependent anticipations may differ from action-independent anticipations. In evolutionary–developmental terms, we may ask to what extent anticipatory behaviour is structured by the history of the species or by the development of an organism. And, in a cognitive modelling context, to what extent are anticipatory estimations further shaped by individual experience and learning? All these questions indicate the variety of factors by which anticipatory processes may be distinguished and modelled in biological systems.

The upshot here is that different types of anticipatory mechanisms account for the processing of different kinds of information. What all these types of anticipation have in common is that they involve a form of prediction of future states, a prediction that is somewhat based on prior experience. The key difference between these various forecasting mechanisms is the nature of the assertive mechanism in relation to the information being processed.

From this perspective, we see what it means to say that there is no obvious or intrinsic link between a stimulus or stimulus structure and our perception of that stimulus. Rather, we have adjustable perceptual relations where input cues are integrated in terms of their temporal and contextual associations with other external sensory cues, internal hidden states (experience and memory-based, or internally inferred), expectations, or predictions, and feedback processes of error correction. As a result, the perception of the input and its value is not invariant but highly contingent.

5. Conclusions: Perception as a Measure of Changing Signal Ratios and Expectancy Effects

Higher flexibility in the processing and evaluation of perceptual information such as in olfaction makes sense when we think of perception as a dynamic process that organisms use in order to navigate in an ever-changing environment. Such navigation commands not only constant attention but also choices between different options and behaviourally selective responses to contextual clues. It would actually be catastrophic for most of our choices if we were to perceive stimuli in a strict input–output-related fashion, without any regulatory principles that allow us to contextualize and discern the subtle differences in these cues before we selectively act on them. Olfaction in particular is deeply action-based and is shaped by perceptual biases, which makes sensory measurement in olfactory psychophysics notoriously difficult (Keller and Vosshall 2004; Barwich and Chang 2015).

Nevertheless, emphasis on the flexibility and contextuality of perception is not a view of 'anything goes'. The governing principles of perceptual processing are bound to the physiological organization of organisms, their evolutionary species-specific history, and the influence of individual experiences and learning. These processes are contingent but not random. After all, we do end up with fairly stable and generalizable perceptions.

Perceptual stability, as this chapter has put forward, is based on the successful integration of stimulus clues into experienced and predictable patterns. The regularity of these patterns reflects the ratios, combinations, and proportions of selected features in the environment.[11] Their perception is further shaped by how these ratios are interpreted within organismal response spaces. These spaces represent associations of sensory cues and of their affective options, and the nature of these associations depends on the organismal states in which the cues are experienced and anticipated.

Success, as in the successful integration of stimulus ratios within a sensory system, is an interesting notion. It inevitably implies some form of evolutionary success. Does success also imply a notion of correctness? From a process perspective, I think the answer is not about whether it does, but about *when* it may imply accuracy. As I have argued, an answer cannot be approached in terms of odour objects. It must be modelled after the processes that translate distal into proximal stimulus patterns, and this translation is fundamentally determined by top-down processes in term of expectancy effects.

As for the case at hand, olfaction seems particularly apt to analyse the perceptual relations between variable stimulus ratios, selective biases introduced by experience, and behavioural responses. As mentioned at the beginning of this chapter, the olfactory system is incredibly precise at the level of physical stimulus detection (the smallest chemical impurities can cause significant differences in the perception of odour qualities). It is also immensely flexible when it comes to stimulus evaluation and integration of olfactory cues into various perceptual contexts, on the basis of differences in exposure and experience (i.e. in cases of cross-modal perception, verbal labelling, conditioning, personal experience and memory, and so on). This shows that perceptual biases are not a failure of the level of sensory detection but an inherent and constitutive part of the processing system.

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[11] An epistemological argument for the measurement of sensory qualities as structurally relational properties is presented in Isaac 2014.

From a process perspective on perception, perceptual representation is about informational content. Such content does not necessarily represent perceptual instances as classes of perceptual objects, for instance as ‘odour objects’. Instead we experience ‘odour situations’ that provide a measure of how certain cues are related to each other (e.g. temporally, combinatorially, causally) and are given a certain value (e.g. pleasant, putrid). What constitutes the informational content of odour situations is variable and contingent upon the associations that are formed between certain ratios and combinations of inputs and the expected value of their (potential) interactions. Any interpretation and the potential for perceptual generalizations of such measures into kinds of perceptual qualities is grounded in organismal construction and needs, as well as in experience and learning; it is action-relative as well as memory-based and must be understood with respect to the interaction of the perceiving organism with its environment.

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Everything Flows

Towards a Processual Philosophy of Biology

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