nature reviews psychology

https://doi.org/10.1038/s44159-024-00382-1

Review article

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Evaluating cognitive penetrability of perception across the senses

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Abstract

A central question about the human mind is whether perception is an encapsulated process driven purely by sensory information or whether it is intricately linked with cognitive processes. This debate about the cognitive penetrability of perception is discussed in psychology, cognitive neuroscience and philosophy. Thus far, the debate has centred on vision, without major attempts to examine other senses. In this Review, we provide an overview of the key empirical evidence about cognitive penetrability of perception in vision, audition, somatosensation (including proprioception and pain perception), vestibular perception and chemosensation (gustation, chemesthesis and olfaction). We conclude that many (but not all) of the senses are cognitively penetrable. Specifically, cognitive penetrability seems to vary with the extent to which a sense is intrinsically multimodal, the extent to which it receives indirect cognitive influences, and whether hedonic evaluation is an integral aspect of the perceptual experience. We suggest that the debate about cognitive penetrability needs to be more differentiated with respect to the sensory modality of the perceptual experience and the diversity of cognitive influences on that modality.

Sections

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Introduction

Perception of the world by human senses might be influenced by one's thoughts, knowledge and memory contents. Alternatively, perception might operate independently of cognition. These two possibilities lie at the core of the debate about the 'cognitive penetrability' of perception and have been intensely discussed in psychology, cognitive neuroscience and philosophy of mind[1–9]. This debate relates directly to key questions in philosophy and brain sciences. For instance, if cognition influences perception, then perception would be a product of subjective experience and thought processes rather than a veridical representation of the outer world. Furthermore, cognitive penetration calls into question the distinction between cognition and perception and whether brain areas are exclusively dedicated to perception or cognition or, alternatively, if intertwined processing across brain areas means an elimination of a clear distinction between cognition and perception.

The debate has recently gained momentum, fuelled by philosophical proposals that argue that cognition and perception have distinct properties and formats[10], which raises the question of exactly how cognition and perception interact. The debate on cognitive penetrability of perception has to be resolved by considering empirical data, including evidence from neuroscience, which some previous discussions have neglected[2]. In addition, the debate about cognitive penetrability has so far almost exclusively focused on visual perception. Thus, specific characteristics of vision might have inadvertently shaped the debate.

Perception happens beyond just vision, so a comprehensive examination of cognitive penetrability should consider all senses to integrate evidence across subfields. Because different perceptual systems might be differentially susceptible to cognitive influences, here, we push forward the debate on the cognitive penetrability of perception by comparing different sensory modalities. If perception is truly impenetrable by cognition, it should be impenetrable across the senses. By contrast, if cognition does penetrate perception, the degree of penetrability might vary across the senses. Thus, fleshing out the differences and commonalities in cognitive penetrability between the senses based on empirical psychological and neuroscientific evidence has the potential to substantially advance and clarify the debate.

In this Review, we first briefly summarize the key arguments for and against cognitive penetrability of perception and provide an operational definition of cognitive penetrability. We then present the key empirical evidence separately for vision, audition, somatosensation (including touch, proprioception and pain), vestibular perception and chemosensation (including gustation, chemesthesis and olfaction). Subsequently, we step back to synthesize whether, for each sense, the evidence speaks for or against cognitive penetrability. Finally, we conclude and discuss future research directions.

Arguments for and against cognitive penetrability

Cognitive penetrability is usually defined as the influence of a higher cognitive state (such as memory contents, abstract knowledge, beliefs or intentions) on 'perceptual experience'. Perceptual experience is what philosophers of mind refer to as the phenomenal character of perception: 'what it is like' to experience a particular percept as the perceiver[4].

At the very core of the debate lies the intuitive idea that perception and cognition are separable processes in the mind, of different 'kinds' and with different qualities[10] (Fig. 1). Drawing a theoretical distinction between perception and cognition does not per se argue for or against cognitive penetrability but it lays the groundwork for presupposing different systems for cognition and perception and the question of how these two systems interact.

Early proponents of cognitive impenetrability usually presumed a strongly modular organization of the mind. Specifically, they argued that perceptual experience is the output of an 'informationally encapsulated' early sensory module that is separate from cognition[11,12] (Fig. 1a). In these early works, encapsulated modules are conceptualized as computational mechanisms that are specific to a cognitive domain, hardwired, computationally autonomous and restricted to a set of inputs without access to information stored in other modules[11]. Because of this clear functional distinction between modules, the sensory module creates a perceptual experience without any direct influence of cognition. Yet, even early proponents[12] admitted that cognition could influence perception via indirect mechanisms such as attention-driven enhancements of feature perception. Despite this admission, the view of an encapsulated and impenetrable perceptual module is still defended today[2].

The idea of a strong modularity of the mind originated from evidence for the functional specialization of brain areas. For example, neuropsychology and early neuroimaging showed that perceiving colours activates brain area V4 and that lesions to V4 lead to a deficit in colour perception[13,14], whereas cognitive processes, such as decision-making, activate the frontal cortex and lesions thereof lead to related cognitive deficits[15]. Accordingly, it was concluded that perception and cognition happen in separate and independently operating brain areas.

The time course of brain activity has also been used to argue for cognitive impenetrability. Neural data revealed that early sensory areas extract basic sensory features quickly after perceptual stimulation and higher-level sensory areas process more complex information later on[16]. These data led some theorists to claim that basic perceptual processes happen within the first 100 ms of processing, which is too rapid for any cognitive influences from higher brain areas such as the frontal cortex[7].

Another argument for cognitive impenetrability comes from the phenomenology of visual illusions. Famously, the Müller–Lyer illusion contains line segments of the same length that appear to have different lengths (Fig. 2a). Even if an observer is familiar with the illusion, the cognitive knowledge that the two lines are of equal length does not overcome the illusory percept. Thus, it is usually concluded that the illusory percept is impenetrable by cognitive knowledge.

Proponents of cognitive impenetrability also argue that the evidence for cognitive penetrability is insufficient and inconclusive, and therefore the presupposition of an impenetrable sensory module must be true[2]. For example, some theorists and experimentalists have argued that psychological evidence for the effects of cognition on perception reflect changes in the cognitive judgement of perceptual experience not the experience itself[2]. Further, they argue that certain processes (including feature-based and object-based attention as well as object recognition) are part of the perceptual module and therefore influences of these processes on perception do not count as cognitive penetration. Here, it becomes clear that one of the key sticking points in the cognitive penetrability debate is where to draw the boundary between perception and cognition. If the perceptual module is defined to encompass many high-level processes, then it is easier to argue against cognitive penetrability because cognitive processes within the module are defined as perceptual. By contrast, if the boundary for what counts as perception is set sufficiently low, then many top-down influences can count as cognitive penetration.

Proponents of cognitive penetrability often argue against a clear-cut boundary between perception and cognition. Some question the existence of a cognition–perception boundary altogether[3,17] (Fig. 1c). Others argue that, even if one can maintain a distinction between predominantly cognitive processes (such as abstract mathematical reasoning) and predominantly perceptual processes (such as seeing a single light in the dark), the majority of functional everyday perception results from an interplay of different intermediate processing stages along the perceptual processing hierarchy, and is therefore a mixture of cognition and perception[5,9,18] (Fig. 1b).

Empirical evidence supports the view that almost all percepts are a product of both bottom-up sensory processes and top-down cognitive processes. For instance, modern neuroscience evidence shows that, although there is functional specialization of brain areas, strict modularity of brain function, and particularly the idea of informational encapsulation, is inaccurate. At the anatomical level, the vast majority of cortical brain areas are heavily interconnected through lateral, short-range and long-range connections[19]. These connections make the existence of informationally encapsulated modules highly implausible. Instead, complex, recurrent dynamics of interacting bottom-up and top-down processes sculpt neural processing throughout the sensory hierarchies (Fig. 3). These dynamics are essential for functional perception and influence all perceptual processes throughout the time course of processing, even shifting how neurons respond to the same sensory inputs to reflect top-down expectations and predictions[20–24]. Thus, attempts to draw a strict boundary between perception and cognition are motivated by theoretical arguments that seem to ignore modern knowledge about brain organization.

However, the constant information exchange across different brain areas does not mean that each brain area arbitrarily interacts with every other brain area. Instead, information exchange is confined by structural and functional brain connectivity that plastically evolves during development and learning. The example of the Müller–Lyer illusion nicely illustrates that not any cognitive knowledge (for example, knowing that the two horizontal lines are of equal length) can influence any percept (that the lower line looks longer, Fig. 2a). In fact, some theorists have argued that the Müller–Lyer illusion demonstrates a case for cognitive penetrability: growing up in human-made, mostly rectangular environments results in learned associations about the length of edges of floors and walls consistent with the upper line being longer. Thus, the Müller–Lyer illusion can be seen as a consequence of a cognitive inference about line length induced by the flanking arrowheads[9,25]. This example demonstrates that different penetrating factors need to be distinguished; not every piece of cognitive knowledge can influence every perceptual experience. However, the reverse inference — that the lack of a specific cognitive influence implies that no cognitive state can penetrate perception — does not seem valid either, particularly when considering the evidence on recurrent information exchange and the evidence reviewed below.

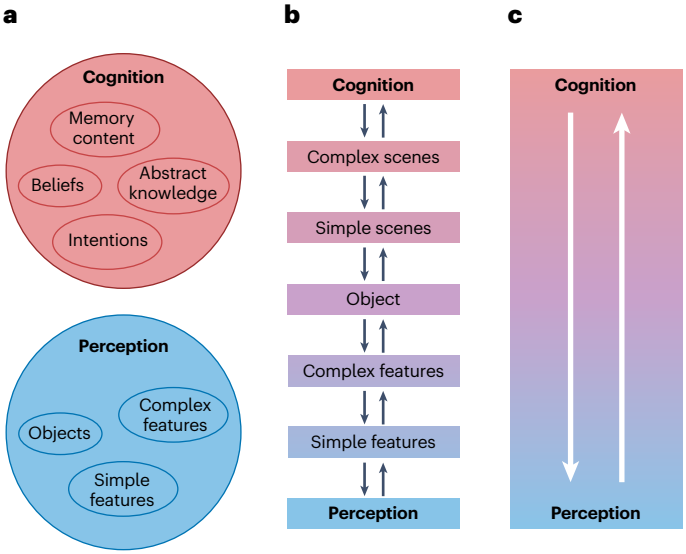


Fig. 1 | Possible relationships between cognition and perception. a, The impenetrability thesis. Perceptual processes, including low-level and high-level perceptual processes, happen in an 'informationally encapsulated' module that is separate from and impenetrable by cognitive processes[2,11,12]. **b**, One penetrability thesis. The theoretical distinction between high-level cognitive processes and low-level perceptual processes is maintained but with a constant exchange between many intermediate processing stages in which cognition and perception are intermixed. Thus, cognitive penetration of perception is possible, even if not from every stage[5,9,18]. **c**, Another penetrability thesis. The border between cognition and perception is gradual and fuzzy, no clear boundary is defined, and therefore penetration can happen in both directions[3,17].

Penetrating factors

There has been considerable debate on what counts as a cognitive factor and therefore what can be considered to penetrate perception. Feature-based and object-based visual attention have typically been included as penetrating factors as they depend primarily on a task or knowledge[26], which are considered cognitive. However, shifts of visual spatial attention have typically been excluded as penetrating factors[4] because they can influence perceptual experience in a manner independent of cognitive content[27] and may change the state of the sensory organ similar to eye movements. Although discounting spatial attention as a cognitive factor seems intuitive in vision, it might make less sense in audition. Spatial and non-spatial auditory attention influence early auditory processing in a similar way, so the distinction between spatial auditory attention and other forms of auditory attention is unclear. Changes in the external stimulus (such as brightness or loudness) that automatically draw exogenous attention are also usually excluded as penetrating factors. Internally driven, endogenous attention is a more controversial case because endogenous attention can be purely spatial (as in the instruction to 'attend left'), temporal ('attend now') or cognitively driven ('look for the red bike' or 'listen to the teacher's voice'). Similarly, internally generated mental imagery can have more or less cognitive content[28]. For the purpose of our Review, we focus on influences that carry cognitive content. Cognitive content includes, for example, semantic memory content, abstract or conceptual knowledge, or beliefs or intentions.

There is a lot of evidence that temporal expectations, spatial expectations and priors (the assumed probability of each observable state of the environment) influence perception in touch, audition and vision, and potentially in olfaction. However, the extent to which these factors count as cognitive states in the traditional definition of cognitive penetration is unclear. Priors reflect knowledge about the world but the information stored in priors is not always cognitively represented. For example, visual perception of tilted lines is influenced by a strong prior assumption that lines are typically either vertically or horizontally oriented[29] and prior assumptions about the location of the limbs are deeply embedded in the tactile system[30,31]. Yet, even though

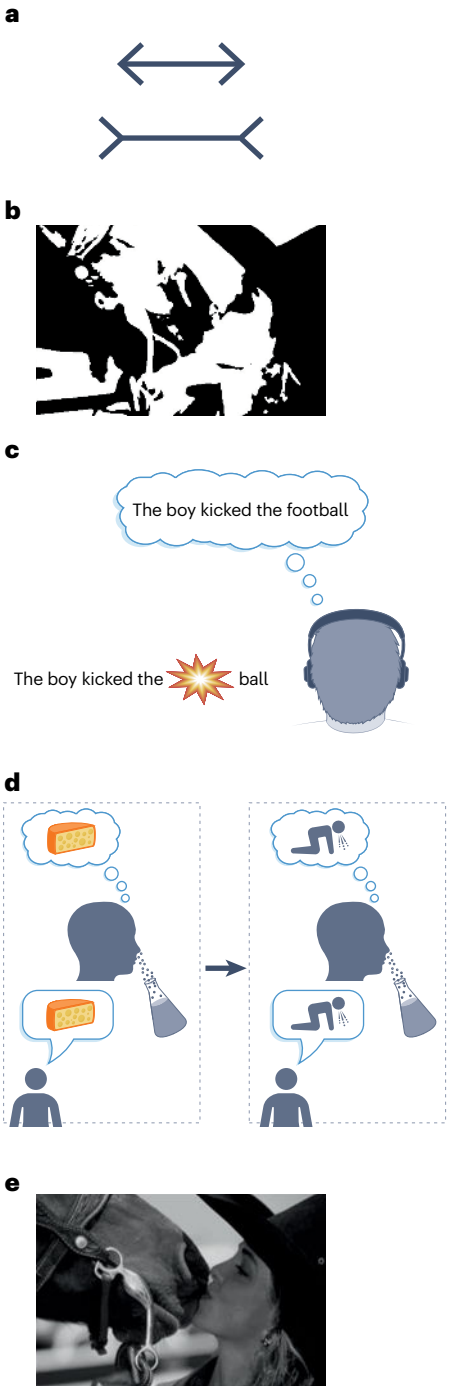


Fig. 2 | Top-down effects in different senses. Top-down effects in vision: **a**, In the Müller–Lyer illusion, the two horizontal lines are of equal length but the upper line is usually perceived as shorter than the lower line due to the angled lines. Knowledge of the line length does not change the illusory perception of different lengths. **b**, This two-tone image seems like a meaningless assembly of black-and-white patches but becomes immediately recognizable once one has seen the full grey-scale photograph (part **e**) that provides contextual, high-level information. **c**, In phonemic restoration, a listener perceives continuous speech from noise and fills in the missing content based on the surrounding context, often without being aware of a gap. **d**, Top-down effects in olfaction: participants sample an odour that is labelled as either 'parmesan cheese' or 'vomit'. When the label differs, participants do not recognize the odour as being identical to the one they previously smelled[214]. **e**, Full grey-scale photograph from which the image in part **b** was derived. Parts **a**, **c** adapted from ref. 42, Springer Nature Limited.

these priors might mirror the statistics of the world, and are therefore observable, most people whose perception is influenced by these priors would be unable to list them. Thus, most priors influence perception in the absence of explicit conscious awareness, whereas influences from cognitive content can, but do not have to, be accompanied by conscious awareness of that content.

The extent to which perceptual learning (long-term learning of statistical regularities arising in one's sensory environment[32]) counts as cognitive penetration of perception is also up for debate. For example, a bird watcher learning to recognize a species of bird goes through a learning process that involves explicit cognitive processing of the combination of features characterizing the bird before the recognition process becomes automatic and therefore, to some extent, perceptual. Similarly, in olfaction, sweetness becomes an intrinsic perceptual property of odours such as vanilla after many instances of associative learning in which sweet and vanilla are experienced together. Some theorists argue that cognition penetrates perception at least during perceptual learning because cognitive knowledge about, for example, the features of a bird, impacts later perceptual recognition of the bird[8]. However, other theorists have argued that perceptual learning can happen within the encapsulated perceptual module as being part of basic perceptual mechanisms, similar to feature-based attention or object recognition[2,12].

Whether emotional influences count as cognitive is also unclear. Although emotion and cognition are intricately intertwined, they are partly subserved by distinct brain pathways[33]. Emotions have sometimes been conceptualized as perceptual[34] and, in some sensory modalities, the hedonic evaluation of a percept (such as the pleasantness of touch or spicy food) is an integral part of the perceptual experience. It is therefore difficult to classify emotions as clearly cognitive. Emotional penetration of perception has partly been reviewed elsewhere[35] and deserves its own discussion outside the scope of this Review.

Overall, no firm conclusion can be drawn in either direction for any of these areas and each reinforces that the debate on cognitive penetrability crucially hinges on what counts as cognitive.

Perceptual experience and evaluation

Another sticking point of the debate is what exactly is being penetrated or influenced by cognition. Philosophy of mind defines cognitive penetration as a cognitive influence on the phenomenology of perceptual experience. Proponents of cognitive impenetrability have often argued that it is not the perceptual experience itself that is being penetrated but rather the judgement of this experience, which they argue is a cognitive, post-perceptual process. Accordingly, many psychological studies that show cognitive influences on perception have been discounted as involving such an influence[1,2]. From an experimental point of view, it is not easy to disentangle perceptual experience from its judgement. In the laboratory, measuring perception usually requires participants to explicitly report aspects of their subjective percept (for example, the length of a line), which inevitably involves a conscious and cognitive judgement of the percept (for example, whether the line is longer or shorter than a reference line). These reports are susceptible to potentially cognitive response biases in decision-making. Thus, biased

responses in a behavioural experiment might not necessarily reflect perceptual biases. One way to circumvent this problem in behavioural experiments is to focus on perceptual sensitivity, which enables the dissociation of perceptual effects from response criteria, or to combine perceptual judgements with additional variables that distinguish perceptual biases from response biases (Box 1). Another approach is to measure physiological correlates of perception, such as microsaccades or pupil dilation, that cannot be voluntarily controlled and are therefore unlikely to be affected by response biases. Finally, changes in neural correlates of early stages of perception, such as activity in early sensory cortices or early components of electrical brain activity, are unlikely to be impacted by cognitive judgement processes and therefore provide good evidence for cognitive penetrability. We focus on evidence from these and similar paradigms that can be unambiguously attributed to changes in the actual percept.

Evidence across the senses

For the purpose of this Review, we define cognitive penetration as a change of perceptual experience through the influence of a higher cognitive content such as a semantic memory content, abstract or conceptual knowledge, or a belief or intention (in line with ref. 4). The change in perceptual experience cannot be caused by a change in external stimulus conditions (such as lighting or background noise), a change in a sensory organ (such as eye movements, sensory loss or pathological conditions), or shifts of exogenous or spatial attention. With respect to the penetrated perceptual experience, we take the perspective of experimental psychology and restrict perceptual experience to experimental measures of objective task performance. We distinguish between veridical changes of perceptual experience and response bias of that perceptual experience.

We focus on senses with a dedicated sensory system in the brain (and as such exclude interoception, for example). Thus, we discuss perceptual experience in vision, audition, somatosensation, vestibular processing and chemosensation (Fig. 2). We do not discuss cross-modal interactions or multisensory integration in detail because such mechanisms have been reviewed elsewhere[36,37]. In cases where sensory experiences are inherently multisensory (for instance, flavour perception is a combination of taste and smell), we focus on the multisensory perceptual experience rather than integrative aspects.

Vision

In vision, evidence in favour of cognitive penetrability has been reviewed and discussed in depth by both philosophers and psychologists[1,3,5,6,8,9]. Many studies were not designed with the cognitive penetrability thesis in mind and therefore did not explicitly distinguish perceptual measures from response biases. However, many other studies do demonstrate changes in perceptual experience due to cognitive influences independent of response biases.

Studies measuring visual sensitivity (d') present substantial evidence for cognitive factors influencing vision. For example, high-level cognitive image content cued by spoken words, verbal cues, or naturalistic sounds increase visual sensitivity and facilitate image recognition of masked stimuli or stimuli suppressed from visual awareness relative to uninformative or semantically incongruent stimuli[38–41]. Similarly, object recognition in two-tone, black-and-white images is difficult without prior knowledge (Fig. 2b). Previous exposure to the full grey-scale image (Fig. 2e) increases visual sensitivity to edge detection in these images, even when the images are task-irrelevant, attention is controlled and visual stimulation remains identical[42] (see also ref. 43 for confirmatory results not measuring d' but with additional electroencephalography evidence). Furthermore, in an ambiguous display in which moving balls can either bounce or cross, imagined sounds of colliding objects promote the visual perception of bouncing balls[44]. Thus, both early visual feature detection and object recognition in noisy and ambiguous visual situations are enhanced by cognitive information while ruling out confounds of response biases.

Another way to circumvent the problem of response biases is to measure neural or physiological correlates of early vision that cannot be voluntarily controlled. Given that the vast majority of visual perceptual experiences, even when imaginary or unconscious, involve the early visual cortex[28,45] and the eyes, cognitive influences on these respective correlates are very likely to also impact perception. For example, the involuntary pupil response has been shown to be modulated by higher-level cognition, even when controlling for general effects of attention and arousal[46]. For example, pictures containing a sun lead to smaller pupil size (in expectation of higher luminance) than pictures containing a moon, even if the actual luminance of the pictures is the same[47–49]. Similarly, listening to words that convey a sense of brightness or darkness (such as 'day' or 'night')[50], imagining bright or dark objects[51], and maintaining bright or dark objects in visual working memory[52] modulates pupil size according to whether a bright or dark visual stimulus is expected, even when actual visual input is minimal or absent. Even words with a positive meaning (such as 'victory') elicit pupil responses in expectation of brightness compared with words that have negative meaning[53]. Together, these findings indicate that high-level cognitive concepts modulate the visual system at the very early level of the pupil.

Neural representations of visual stimuli, particularly in the early visual cortex, are not under voluntary control and are therefore unlikely to be directly affected by response bias. Cognitive influences on these neural visual representations are often measured as changes in functional MRI activity patterns using multivariate pattern analysis[54]. For

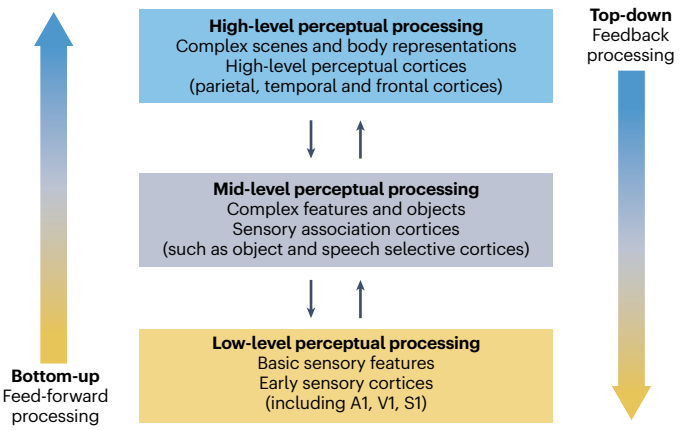
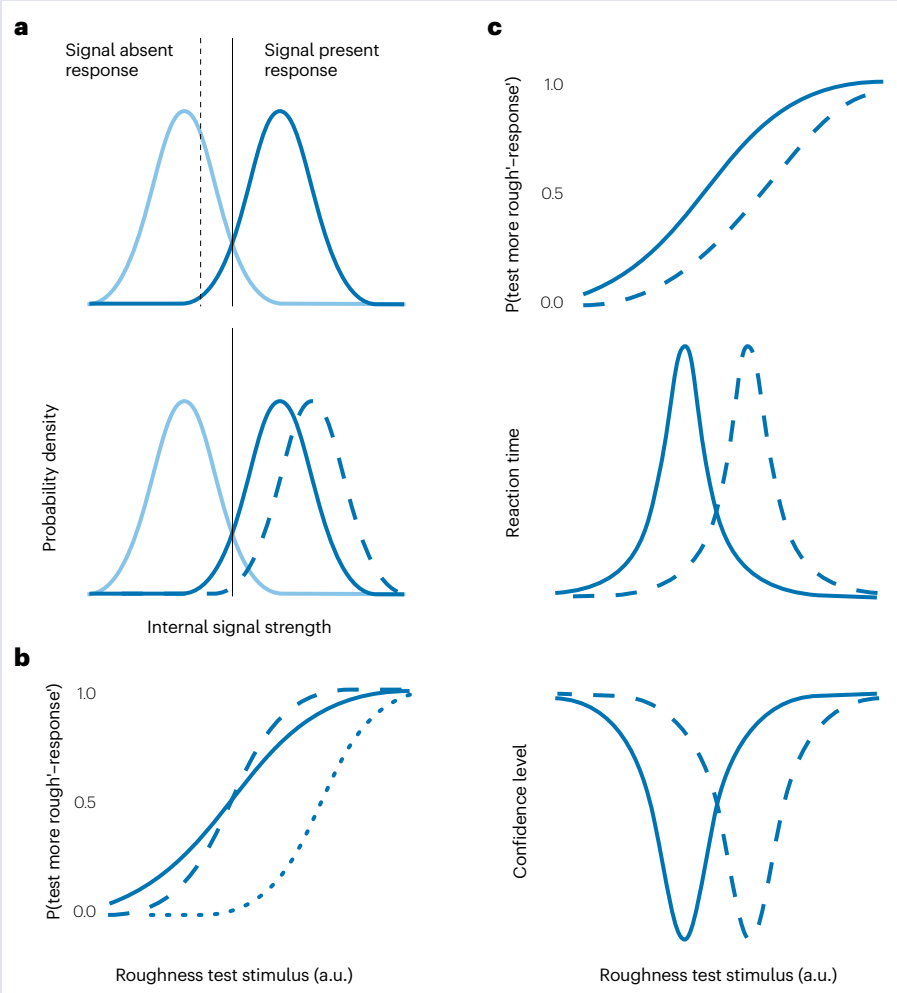


Fig. 3 | Hierarchical recurrent perceptual processing in the human brain. Perceptual processing in vision, audition, olfaction, gustation and somatosensation occurs along a hierarchy through low-level (yellow), mid-level (grey) and high-level (blue) processing. Brain areas responsible for the different processing stages are anatomically and functionally highly interconnected, and information constantly flows in both directions, bottom-up via feed-forward connections and top-down via feedback connections to create conscious functional perception from complex and multisensory information. The vestibular system does not have a dedicated unimodal sensory cortex (as depicted here) but is instead supported by a widespread subcortical and cortical network.

Box 1 | How to reliably identify changes in perception



Behavioural studies that claim cognitive penetrability of perception need to demonstrate changes in the perceptual experience and rule out changes in the emotional or cognitive evaluation of that perceptual experience. Both a change in the response criterion of participants (the amount of sensory evidence internally required for a response; figure part **a** top, solid and dashed vertical line), which would not be classified as cognitive penetration of perception, and a change in their internal stimulus representation (figure part **a** bottom, solid and dashed curves), which would count as cognitive penetration of perception, can influence the probability with which participants report the presence of a stimulus (or of a difference between stimuli). Signal detection theory[241] enables experimenters to isolate the sensitivity of participants to sensory information (their ability to detect sensory signals in the presence of sensory noise) from their response criterion and therefore reliably identify changes in perception.

Moreover, psychophysical studies using a forced choice design can measure changes in the just noticeable difference — the minimal change in the stimulus the individual can reliably perceive (figure part **b**, dashed versus solid curves) — independent of shifts in perceptual and response biases (figure part **b**, dashed versus dotted curves). For example, instead of requiring participants to report whether they perceived a difference between the roughness of two haptic stimuli, participants report which of the two stimuli felt rougher. The latter question measures the ability to detect differences between the stimuli by varying the roughness of one of them and without explicitly asking for differences. Changes in sensitivity or just noticeable differences due to cognitive information provide strong evidence for the cognitive penetrability of perception.

However, cognitive influences on perception will not necessarily result in a change in these sensitivity measures. For example, even if, owing to a change in cognitive factors, all textures feel a little rougher, it might not be easier to distinguish between them, leaving the just noticeable difference unchanged. The shift in the percept towards a rougher (figure part **c** top, solid versus dashed curves) stimulus can reliably be quantified using psychophysics, ideally in a forced choice discrimination or matching task rather than using ratings alone. Yet, a shift in the responses of participants in itself does not always provide conclusive evidence. If, in our haptic example, one test stimulus is similar to sandpaper but the other is not, participants can always identify which one is which. If they now exhibit a tendency to categorize the sandpaper stimulus as rougher than the neutral one but do not do so for a stimulus reminiscent of carpet, it is impossible to know if their knowledge about sandpaper and carpets changed their actual percept, or just their tendency to report a stimulus as rougher than the neutral one. If participants indeed perceive the stimulus differently, the reaction time distribution (figure part **c** middle, solid versus dashed curves) should shift with the psychophysical curve. Thus, a shift in the percept should lead to a shift in the mode of the reaction time distribution that parallels the shift in the forced choice responses (for an example, see ref. 242). By contrast, a change in response bias should have hardly any effect on reaction times. To further support such a conclusion, experimenters can collect confidence ratings, indicating how confident participants are about the accuracy of their response. If the percept of a participant changes, their confidence in the evaluation of this percept should change, too[243] (figure part **c** bottom, solid versus dashed curves).

example, there is accumulating functional MRI evidence that the cognitive demands of tasks directly impact neural visual representations of identical stimuli, independent of attention, and all along the visual hierarchy down to primary visual cortex V1 (for a review, see ref. 55). For example, V1 and V2 activity patterns in response to the same animal image differ significantly depending on whether the task is to categorize the image as a dog or a mammal; even mere anticipation of the task changes activity patterns in the early visual cortex before the visual stimulus is shown[56]. In other similar studies, task (such as discriminating colour or discriminating tilt) modulates neural activity patterns for identical objects in the early visual cortex as well as along the ventral visual object-processing pathway[57]. These results suggest that early vision gets tuned to the features of the environment that are particularly task-relevant and that behavioural goals directly impact visual representations of identical objects. Many visual brain areas upstream from V1 and equally responsible for functional visual perception, such as high-level visual cortices[58] and category-selective regions for face[59], word[60] and object[61] recognition, are influenced by task.

Apart from tasks, many cognitive activities modulate neural representations in the early visual cortex via top-down feedback. These include active mental imagery[62], visual expectations[63,64], memory retrieval[65], learned conceptual associations[66], working memory content[67,68], action execution and action preparation[69,70], haptic shape exploration[71], and listening to complex natural sounds[72,73]. These changes in neural representations in early visual cortex do not occur with any unspecified cognitive activity (and therefore cannot be attributed to attention) but rather are specific to content or stimulus. Furthermore, many cognitive influences lead to a specific change in neural tuning[66] or a sharpening of the precision of visual representations[64,70,72]. Many studies present strong effects of top-down neural processing in vision[20,74,75] in accordance with evidence for the recurrent stream architecture of the visual system[21–24], which demonstrates that visual perception always involves both bottom-up and top-down processing (Fig. 3).

These results render the possibility of an informationally encapsulated visual module highly implausible. Instead, accumulating behavioural and neural evidence supports the idea that many different types of cognitive activity have a deep and manifold impact on visual perception and visual brain processes. These impacts occur across all visual brain areas and at the level of the eye and support the close integration of the visual system with many high-level cognitive brain systems.

Audition

Unlike in vision, few studies in audition have directly addressed whether auditory perception exhibits cognitive penetrability. Instead, evidence comes from a range of studies exploring specific questions such as the influences on sound perception from expectations based on probable sound structure, explicit cueing, short-term statistics and long-term learning. Experiments not specifically designed to address the cognitive penetrability of audition nonetheless offer behavioural and neural evidence relevant to the question.

Top-down expectations strongly influence auditory perception across different experimental paradigms. In the phonemic restoration paradigm, listeners hear speech interrupted by temporal gaps that are filled in by noise. Instead of hearing discontinuous speech, listeners subjectively perceive complete words and do not realize that their knowledge and expectations supplied the missing information (Fig. 2c). Moreover, listeners show improvements in objective measures of speech perception. Indeed, filling the gaps in with noise makes listeners perceive the interrupted speech as if the missing phonemes were actually present[76] (for a review, see ref. 77). Simpler non-speech stimuli display a similar 'continuity illusion': listeners perceive a sound that is interrupted by silence as continuous if noise is presented during the gap[78,79]. Experiments using similarity ratings[80] and measures of perceptual sensitivity[81,82] demonstrate that these phenomena represent true changes in the perception of interrupted sounds, not simply a bias in how sounds are labelled. In both phonemic restoration and the continuity illusion, high-level knowledge of and expectations about sound structure override pure sensation to dominate perception. More generally, preceding speech inputs enable prediction of upcoming speech at the level of phonemic, lexical and semantic structure[83]. Indeed, such top-down expectations even influence speech perception retroactively, changing perception of preceding ambiguous speech to be consistent with later inputs[84,85].

Explicit priming also influences auditory perception. Naive listeners might not even recognize that severely degraded speech (such as noise-vocoded speech or sine wave speech) is a speech signal. Priming with a preview (acoustic or visual) of the speech content before the degraded speech qualitatively changes perception so that the degraded sound is heard as speech[86–88]. Moreover, such priming of degraded speech, as well as priming from semantically related content, improves objective measures of speech intelligibility compared with when the same speech is presented without being primed[86–88], confirming a true perceptual change. Semantic priming by a related word, sound or picture also impacts perception of non-speech, environmental sounds, speeding up identification reaction times and reducing error rates compared with when there is no preceding prime[89–91].

Auditory perception also varies with experience and learning across a range of time scales. Rapid learning is exhibited in listener adaptation to talker accent, which occurs as rapidly as over the course of a few words[92–96]. Explicit cueing of talker identity enhances such effects, improving speech understanding compared with when the same accented speech is heard without cognitive knowledge of the talker identity, demonstrating a role for explicit knowledge on perception[97]. Long-term learning also strongly influences perception. For instance, listeners show a remarkable sensitivity for implicitly learning random patterns of tones or noise exemplars such that, when tested (even weeks) later, the previously heard examples are more easily detected than novel, similar patterns[98–102]. Together, these studies demonstrate that learning directly influences how sounds are perceived.

In addition to behavioural results, neural evidence supports the idea that cognitive processes interact directly with auditory sensory representations. During phonemic restoration, activity in the auditory regions that represent the acoustic properties of speech (including the middle temporal gyrus and superior temporal sulcus[103]) reflect the illusory percept and not the disrupted sensory inputs. These results provide direct physiological evidence that top-down expectations alter speech perception[103–105]. Similarly, the auditory cortex responds to continuity illusion stimuli as if the input sound were truly continuous[81,106]. When processing degraded speech, priming by a preview of the original speech signal strengthens various neural markers of speech coding in auditory sensory areas[107–109]. Similarly, priming from semantically related content strengthens the neural responses to subsequent degraded speech[88], and semantic priming by a related word, sound or picture changes the neural response to a subsequent sound[89–91]. In speech perception, predictions from preceding speech cause neural feedback onto auditory areas that encode incoming speech inputs,

shaping how these representations code the subsequent speech and directly altering perception of the later speech[110–112]. Such cognitive influences on neural sensory coding are also reflected in learning paradigms. Specifically, the neural coding of sounds changes due to learning: the brain responds more robustly to learned, behaviourally relevant non-speech sounds than to similar but behaviourally irrelevant sounds[113], and, following training on non-native language contrasts, such contrasts evoke stronger neural responses compared to before training[114]. Furthermore, training of novel sound categories changes neural representations such that learned categorical distinctions can be decoded from neural responses in auditory cortex, whereas behaviourally irrelevant distinctions present in the training stimulus set cannot be decoded[115]. These studies provide support for the idea that memory processes feed back onto auditory sensory representations to directly influence the auditory perception of sounds that listeners learn are relevant to their perceptual goals.

Attention modulates neural responses in the auditory system much as it does in vision, enhancing responses to an attended sound stream and suppressing responses to an ignored sound stream (for a review, see ref. 116). Attention can be focused on a spatial location or on non-spatial features, such as timbre, pitch or talker identity[117], although spatial auditory attention more strongly engages prefrontal and parietal cognitive control regions often associated with visual attention than does non-spatial auditory attention[118–122]. Modulatory effects of spatial attention are considered akin to effects changing the sensory organ (such as moving the eye) and not thought to be evidence of cognitive penetrability. Yet, non-spatial auditory attention modulates early auditory sensory responses, such as the N1-P2 event-related potential complex, in a manner similar to modulation by spatial auditory attention[123]. This non-spatial attentional modulation of auditory responses therefore provides a robust example of cognitive influences on perception.

Other auditory paradigms also demonstrate changes in early sensory responses with changes in task demands. For instance, in a match-to-sample task, event-related potentials evoked by statistically identical stimuli differ depending on whether listeners are asked to recall location or pitch[124–126]. Indeed, the kind of information a listener is holding in memory alters the amplitude of sensory-evoked auditory responses, providing another direct example of cognitive factors altering sensory neural coding[127].

Together, these examples suggest that cognitive effects on perception are widespread in the auditory system. Although information moves through an ordered stage of specialized processing regions, each has reciprocal connections with the previous stage. Rather than discrete, separable stages within a hierarchy, the auditory system is better described as a processing heterarchy[128]: information at each stage of processing interacts with and influences information represented at other stages, with no clear simple line separating perceptual from cognitive processing.

Somatosensation

The somatosensory system underlies perception of touch, proprioception (the perception of body posture) and pain. Each of these modalities is processed along specific pathways (which in the case of touch and proprioception merge along the cortical processing hierarchy[129]) and therefore we discuss them separately. Somatosensory perception is anything but an encapsulated process: vision tends to dominate tactile[130,131] and proprioceptive[132] perception, there are strong attentional influences on tactile perception[130], and tactile illusions suggest an influence of prior sensory experience[30,133]. However, few published studies have tested for effects of higher-order cognitive processes on somatosensory perception. Moreover, several of the studies that test cognitive influences on somatosensory perception use measures that are susceptible to response biases, which prevents a final and general conclusion about the penetrability of somatosensory perception. Instead, a differentiated pattern emerges across the different sub-modalities.

Tactile spatial perception requires a representation of the shape of the body. Changes in the representation of body shape can be elicited through conflicting visual information, action feedback manipulations[134], tool use[135] or hypnosis[136]. Manipulations of the perceived size of the body impact the perceived size of objects touching the manipulated part of the body. Perceptually enlarged body parts are associated with perceptual biases towards larger tactile distances[137] as well as better spatial resolution[138] and changes in tactile masking consistent with reduced tactile receptive field sizes[139], which cannot be explained by mere response biases. Thus, a large amount of research suggests that tactile spatial perception is cognitively penetrable. Yet, the cognitive influence is indirect in that changes in the perception of an object are due to changes in the representation of the body part touching the object rather than changes in the representation of the object itself.

Pleasant or affective touch, that is, tactile stimulation elicited by stroking with low velocity and soft pressure[140], is subserved by a different type of receptor and processed along a separate neuronal pathway than mechanical touch[140]. The cognitive penetrability of pleasant touch has high face validity: a caressing touch feels different depending on the identity and presumed intentions of the person doing the touching. However, changes in the pleasantness ratings and bodily reactions to pleasant touch across contexts[141] might exclusively reflect emotional evaluation of the touch and therefore not reflect an effect on perception. In support of cognitive effects on perception itself, the emotional expression of the person stroking the participant affects early components of the characteristic changes in electrocortical activity associated with the tactile stimulus[142]. Similarly, the presumed (not actual) gender of the person doing the touching modulates activity in the primary somatosensory cortex[143]. However, other studies do not implicate primary somatosensory cortices in the encoding of pleasant tactile sensations[144], which has raised the question of why cognitive influences lead to changes in activity in this area. In sum, few studies unambiguously show cognitive penetration of affective touch.

The cognitive penetrability of proprioception has predominantly been investigated behaviourally, in the context of the rubber hand illusion[145]. In this illusion, visual–tactile stimulation, such as synchronous stroking of a visible rubber hand and the participant's real, hidden hand, leads to feelings of ownership of the rubber hand (embodiment) and mis-localization of the real hand towards the rubber hand (proprioceptive drift). These body image-related and proprioceptive effects of the rubber hand illusion are dissociable. Manipulations such as rotating the rubber hand into an impossible position or stroking the real and rubber hands asynchronously influence the embodiment of the rubber hand but do not eliminate the proprioceptive drift[146,147]. Proprioception is drawn towards the location of the rubber hand even when contextual information should prevent this drift. Hence, cognitive processes cannot prevent the integration of proprioceptive and visual information, suggesting that proprioception is cognitively impenetrable[148].

Haptic perception, also known as active touch, requires the integration of tactile and proprioceptive information over time.

Several studies have shown cognitive influences on the haptic perception of textures. However, these results were acquired with questionnaires[149] and psychophysical methods[150] and might therefore index changes in response biases rather than perception. Similarly, knowledge about an object changes haptic perception of that object[151] and the associated network of brain activity[152], yet these results could also be explained by changes in the cognitive evaluation of the perceptual information. Thus, haptic perception might be cognitively penetrable, but additional measures are needed for a definitive conclusion.

Placebo effects are among the most impressive demonstrations of cognitive penetrability of sensory perception — and have enormous practical relevance. Placebo effects refer to any improvements of the well-being of patients on the basis of exposure to cues that are part of a typical medical intervention such as receiving inert sugar pills or visiting a doctor's office. Placebo effects typically do not impact the medical condition (for instance, do not lead to shrinkage of a tumour) rather they alter the subjective symptoms associated with the medical condition[153]. Analgetic (pain-reducing) placebo effects established using subjective measures might reflect response biases or changes in the emotional evaluation of pain and are therefore not considered here. However, analgetic placebo effects are also evident in physiological indicators of sensory processing. For example, neuroimaging studies that combine moderately painful stimuli (such as heat) with a placebo show that placebo treatments impact neural activity in several areas involved in pain perception such as somatosensory cortices, the insula[154] and thalamic nuclei[155]. These areas are involved in early sensory processing of pain and, therefore, modulations in these areas provide evidence for the cognitive penetrability of pain perception. These placebo effects vary with the strength of the analgetic effect[156] and the experimental manipulation of the study[156]. The top-down pathways involved in these sensory modulations are still under debate but there is emerging consensus that placebo effects go beyond conditioning and are rather based on learned cognitive associations[157].

In sum, there is good evidence for the cognitive penetrability of pain perception as well as some tactile perceptual processes and some evidence against the cognitive penetrability of proprioception. Percepts that rely on the integration of sensory information and prior knowledge seem most likely to be penetrable (except for proprioception). By far the strongest evidence for cognitive penetrability of somatosensation comes from studies of analgetic placebo effects. It might be that the complex mechanisms underlying pain perception are more penetrable than, for instance, simple proprioception. Yet, the stark contrast between the small number of studies testing higher-level cognitive influences on other types of somatosensation and the large number of studies testing these influences in pain perception stands out. Ultimately, this disproportionate evidence raises the possibility that the weak evidence for cognitive penetrability in some modalities is simply a consequence of fewer definitive studies addressing the question.

Vestibular perception

Vestibular processing involves interpreting information about one's body motion and orientation in its surroundings and is essential for spatial orientation, balance control and motor coordination. The vestibular system originates from a sophisticated set of sensory transducer organs within the inner ear. Three perpendicular semicircular canals (anterior, posterior and horizontal) detect rotational acceleration of the head along the yaw, roll and pitch axes, and two otolith organs (the utricle and saccule) jointly sense translational acceleration, including gravity. Vestibular signals are relevant to several interactions between the organism and its environment. Specifically, dynamic vestibular inputs from the semicircular canals influence visuo–vestibular interactions for self-motion[158], whereas static gravitational inputs from the otolith organs have a role in path integration and navigation[159].

Unique among the sensory modalities, vestibular inputs lack a clearly defined phenomenological experience. The object represented by vestibular signalling is the body orientation in the three-dimensional space. Consequently, unlike the perceptual experiences induced by specific stimulus objects, such as seeing a red apple, hearing a familiar voice or feeling a mosquito on the skin, vestibular signals do not generate distinct, noticeable or salient perceptual contents. Instead, vestibular signals create a backdrop for all of one's activities. Additionally, vestibular inputs do not project to a primary unimodal cortex, analogous to primary visual cortex V1, primary auditory cortex A1 or primary somatosensory cortex S1. Instead, multimodal convergence between vestibular, visual, somatosensory and proprioceptive cues has been observed in nearly all vestibular relays, including the brainstem vestibular nuclei, thalamus and several areas in the cerebral cortex[160]. Electrophysiological studies in non-human primates have identified a widespread vestibular network, the core area of which is the so-called parieto-insular vestibular cortex[161]. The human homologue of the parieto-insular vestibular cortex is a distributed set of regions including the posterior and anterior insula, temporo-parietal junction, superior temporal gyrus, inferior parietal lobule, and somatosensory cortices (for a review, see ref. 162). With this broad neural distribution, vestibular signals have a role in a range of cognitive functions from sensorimotor control to the highest levels of consciousness[163–167].

Our focus is on whether cognition penetrates pure vestibular processing, that is, behaviour that involves the activation of vestibular peripheral organs, whether via actual movement in the environment or artificial stimulation. We therefore concentrate on vestibular processing related to balance. Balance is the coordination between sensory input, neural processing and motor output that enables an organism to maintain postural stability and equilibrium. This coordination involves integrating information from various sensory systems, including the vestibular system, proprioception and vision, to continuously adjust muscle activity and body position in response to environmental changes. When focusing on vestibular processing for balance, there is no clear evidence supporting cognitive penetrability, meaning that the brain mechanisms responsible for processing vestibular information operate independently of higher cognitive states such as beliefs or expectations.

Although cognitive factors impact the visual channel of balance control[168], the vestibular channel seems to be automatic and immune to cognitive knowledge. When individuals are aware that an upcoming visual disturbance is probably caused by an external source, such as a change in the visual environment, rather than by vestibular self-motion, the whole-body sway balance reflex (an automatic response that stabilizes posture by adjusting muscle activity to counterbalance disturbances or changes in position, thereby preventing falls) is suppressed[168]. However, whole-body sway balance responses to purely vestibular-induced disturbances remain unchanged even when individuals are aware that a vestibular disturbance is likely to occur. Studies have explored the whole-body sway reflex response to a pure vestibular perturbation induced by artificial galvanic vestibular stimulation, a non-invasive technique that stimulates the vestibular nerve via electrodes placed on the mastoids[169]. Often, a bipolar-binaural

configuration is used, in which anodal currents reduce vestibular nerve firing rates and cathodal currents enhance them[170]. Galvanic vestibular stimulation elicits an illusory self-motion sensation that prompts postural adjustments when standing[171,172]. Importantly, the whole-body sway reflex response to this pure vestibular perturbation seems unaffected by whether the vestibular stimulus is self-initiated, predictable or unpredictable. That is, the expectation of a vestibular disturbance, whether through voluntary action or prior knowledge of an event and its timing, does not influence balance responses[173].

The impact of other forms of cognitive modulation, such as changes in cognitive load, on balance control also seems to be inconsistent. Some studies indicate no difference in postural sway when individuals are required to perform a secondary task (dual-task paradigm)[174], whereas others report either a decrease in postural stability[175] or even a slight improvement[176,177]. Taken together, these findings suggest that, if present, the influence of cognitive load on balance control is rather modest.

In sum, current evidence suggests that vestibular processing is resistant to cognitive penetration. This impenetrability can be attributed to the fundamental nature of pure vestibular processing: the vestibular system provides a direct and unambiguous signal to the brain regarding the acceleration of the head in space. This inherent reliability of vestibular signalling might offer a foundation for the brain to adaptively respond to changes in the environment and maintain spatial orientation and balance. The ubiquity of vestibular signalling further reinforces its resilience against cognitive penetration. Given that the vestibular system continuously detects head motion and gravity, it generates a constant sensory flow from early fetal life until death and forms the basis for survival and efficient navigation[166]. As such, the brain might prioritize the reliability of vestibular signals over cognitive influences to ensure behavioural adaptation, particularly in situations in which rapid and precise adjustments are required to maintain balance and avoid potential threats. The robust and reliable nature of vestibular processing might make it less susceptible to cognitive influence compared with other sensory modalities.

Chemosensation

The senses of gustation, chemesthesis and olfaction form the principal detection system in the body for chemical compounds, jointly referred to as chemosensation. The three chemical senses are clearly anatomically separable from each other in their peripheral sensory organs and produce distinct perceptual experiences in the form of taste, chemical irritation and smell, respectively. These will be reviewed separately below given that fundamental differences in neuroanatomy and guiding perceptual processing principles for the chemical senses are likely to impact their cognitive penetrability. These three contributing senses are very closely perceptually integrated when they co-occur in the oral cavity in the context of food consumption. In this context, source allocation to the specific sense is very restricted and an integrated percept emerges, typically referred to as a shared 'flavour sense' arising from the mouth[178,179]. Cognitive penetrability of flavour perception as an integrated form of chemosensory perception will therefore be considered separately from penetrability of the individual senses.

The taste percept arises when water-soluble compounds make contact with gustatory receptors on the tongue, soft palate and pharynx[180], resulting in five known separable perceptual qualities that are each linked to a specific evolutionary benefit or threat (for instance, sweetness indicating the likely presence of carbohydrates, bitterness indicating probable toxicity) and are therefore thought to elicit innate approach and avoidance behaviour (for a review, see ref. 181). There is strong evidence that these innate responses can be regulated by associative learning, in which an initially aversive taste becomes pleasant through association with an object with pleasant features[182–184].

Gustatory receptor stimulation by itself provides insufficient dimensionality for object recognition. For example, when a person experiences nasal congestion that blocks olfactory input, many fruits produce a diffuse sense of sweetness on the tongue, making it impossible to tell apart different fruits (such as a cherry and a blueberry) on the basis of this information alone. Object attribution arises from associations with other sensory input, such as the colour of the food item, its texture and, most notably, the volatile chemicals it releases, which produce an aroma of cherry or blueberry detected in the nose during consumption[185,186]. These cross-modal inputs do not induce changes in the features of taste quality per se but rather in its intensity and hedonic evaluation (pleasantness or unpleasantness). For instance, bitter taste is typically unpleasant but not in the context of the aroma of freshly brewed coffee.

Multisensory effects on hedonic evaluation of gustation are object-specific[187–189], indicating that they are the result of associative learning and, as such, cognitively mediated. Learned associations with specific colours that typically represent a particular object (for instance, red associated with cherry flavour) can result in tastes being perceived as, for example, more intensely sweet or sour, whereas the perceptual quality (sweetness or sourness) remains unchanged. Odours that typically co-occur with particular tastes can increase the perceptual intensity of a gustatory stimulus, a phenomenon known as odour-induced taste enhancement[190]. Thus, high-level knowledge of and expectations about taste do not override sensation to produce a different percept entirely (as it can in senses such as audition) but can change its intensity or hedonic tone.

Few studies have explicitly attempted to identify the location in the processing hierarchy at which these influences arise. The limited existing neuroimaging evidence is in line with impenetrable early sensory representations of taste, with changes in intensity and valence attributions owing to cognitive associations modulating taste-related activation in the orbitofrontal cortex[191–193], and pattern coding in the primary gustatory cortex responding strictly to taste qualities along the five basic tastes[194–196]. Further studies are needed to improve understanding of the neural processing hierarchy that regulates taste-associative learning.

Chemesthesis (the sense of chemical irritation in the skin and mucous membranes) is, like the sense of taste, characterized by low dimensionality: evoked sensations are grouped into those that are experienced as hot and those experienced as cold, with variation referring to the extent of hotness or coldness observed. The sensations are evoked by chemical compounds that activate temperature-sensing transient receptor potential (TRP) channels of cutaneous nerve endings to induce the sensations of coldness (such as menthol, sensed by TRPM8 channel activation) or heat (such as capsaicin, sensed by TRPV1 channel activation) in the absence of actual changes in temperature. During food consumption, chemesthesis arises primarily from stimulation of trigeminal nerve endings in the mucous membranes of the mouth, nose and eyes. The hedonic experience of these can be modified on the basis of learning and experience[197] to be perceived as either pleasant or unpleasant. As such, these perceptions share some common characteristics with the more general experience of pain, as reviewed above. The presence of trigeminal stimulation can increase sensitivity for olfactory and gustatory perception[198–201]. There is some

evidence that peripheral receptor–receptor interactions alter perceptual experience (such as simultaneous chemical stimulation of TRPM8 and TRPV1 inducing the thermal grill illusion in which a moderately warm stimulus and a cold stimulus combined produce a sensation of extreme heat[202]). Furthermore, learned cross-modal associations can modify the intensity of the perceptual experience[203–205]. However, there is no evidence for cognitive penetrability of the sensory quality of the cooling or burning experience induced by chemesthesis. That is, there is no evidence to date indicating that spicy food can induce a cooling instead of burning perceptual quality through cognitive modulation.

In olfaction, sensory experience arises from airborne volatile chemicals that make contact with receptors in the olfactory epithelium at the roof of the nasal cavity, either by sniffing or by being pushed up the throat while food is chewed and swallowed. In contrast to the low dimensionality of gustation and chemesthesis, olfaction is characterized by extremely high dimensionality: humans can functionally distinguish between an almost unlimited variety of odorous stimuli. Yet, labelling and recognition abilities are generally poor for individuals in Western societies, probably owing to a lack of training in associating learned labels with percepts[206] and poor functional–anatomical integration with lexical knowledge[207]. Discontinuities in the mapping of chemical structure to perceived odour are frequently observed[208], in which odours are perceptually grouped together predominantly not by their chemical features but instead by their frequent co-occurrence as part of the same object[209,210], which indicates that odour object perception is highly experience-dependent. For example, although citronellol and 3-octanol are both alcohols, citronellol is perceived as more similar in odour quality to the structurally dissimilar aldehyde nonanal owing to their shared association with lemons, whereas the structurally similar 3-octanol is perceived as more vegetable-like[211].

The olfactory perceptual experience is highly susceptible to cognitive interference[212,213]. Multistable olfactory percepts based on knowledge or cognitive integration of various inputs can arise and switch spontaneously: a given stimulus can lead to a fundamentally different perceptual experience based on the associated label. For example, participants have been shown to experience a combination of butyric and iso-valeric acid as cheese-like when labelled as 'parmesan cheese' but to smell like vomit when labelled as 'vomit'[214,215] (Fig. 2d). Moreover, odour perception changes when odours are presented with particular colours[216,217], sounds[218] or under different metabolic states[185,219]. Evidence increasingly points toward a Bayesian predictive coding framework underlying these findings[220–222] but the plasticity and maturation of these predictions over the life course as well as their functional–anatomical implementation in the olfactory cortical network remain the subject of investigation (for a review, see ref. 223).

Human neuroimaging experiments and rodent studies demonstrate that learned object associations and contextual influences are encoded at the level of the primary olfactory cortex[220,224–227]. Evidence for identity-dependent changes in gamma-band activity even indicates that perceived odour object identity might influence perceptual coding as early as the olfactory bulb[228,229]. Unlike for taste and chemesthesis, high-level knowledge of and expectations about smell can override sensation to produce the percept of a different object representation. As such, behavioural and neuroimaging evidence converges towards a strong argument in favour of cognitive penetrability of the sense of olfaction.

Finally, perceptual experiences related to the chemical senses are tightly conceptually coupled during food consumption and typically perceptually merged into a shared representation of a quasi-synaesthetic 'flavour quality'. Although the merging of gustation, chemesthesis and olfaction into flavour is experience-dependent and therefore mediated by learning, it is highly robust to knowledge. For instance, perceivers are typically unable to experience aroma compounds of foods as arising from the nose, and commonly and persistently attribute reduced flavour perception from blockage of olfactory pathways as 'taste loss'[230]. Furthermore, cross-modal enhancement effects, such as a stronger percept of cherry flavour in a red beverage, persist even when individuals are explicitly told that there is no relationship between the visually elicited object association and the flavour of the beverage, indicating that these associations can arise outside of voluntary control[231].

In summary, the chemical senses are characterized by diversity in peripheral and central processing mechanisms, and there are differences in the extent of available research relevant to cognitive penetrability. The evidence base is strongest for olfaction, where ample evidence exists in favour of cognitive penetrability from behavioural and neuroimaging studies. The evidence base for gustation and chemesthesis is weaker and would benefit from the development of new paradigms specifically suited to address the question of cognitive penetrability in these senses. Meanwhile, although low-level cross-modal effects have been documented, the available behavioural and neuroimaging evidence demonstrates only quantitative changes in gustatory sensations from cognitive influences and no qualitative changes, which might result from the lack of object-processing capabilities of the gustatory sense. The evidence base for chemesthesis is even more limited and provides some weak evidence for cognitive penetrability that also takes the form of quantitative changes in experience. The relative impenetrability of gustation and chemesthesis might provide an evolutionary benefit given the direct link of these sensations to the ingestion of nutrients or toxins. This connection might also explain their pervasive and impenetrable effect on olfaction in the context of flavour binding, where odour experience is substantially shaped by the presence of these modalities.

Synthesis of evidence across the senses

In some senses, the evidence speaks quite clearly for cognitive penetrability, in other senses, it speaks for cognitive impenetrability and, in some cases, the evidence is mixed or simply incomplete. Evidence strongly supports cognitive penetrability of perception in vision, audition and olfaction as well as in pain and tactile perception. Conversely, evidence for cognitive impenetrability exists for proprioception and vestibular processing (apart from modest cognitive load influences on balance control and its visual aspects). Some evidence exists for cognitive influences on haptic perception and influences of the hedonic evaluation on affective touch, taste and chemesthesis but it is difficult to disentangle whether these are true cognitive or more evaluative or emotional influences.

A note of caution is needed when comparing the evidence regarding cognitive penetrability across the senses. The current state of evidence depends directly on the type and amount of research that has been conducted in the respective fields. For example, vision and audition are traditionally more heavily researched than chemosensation, proprioception, and vestibular processing and, accordingly, much more evidence for cognitive penetrability exists in those former modalities. Research on pain perception and placebo effects is of

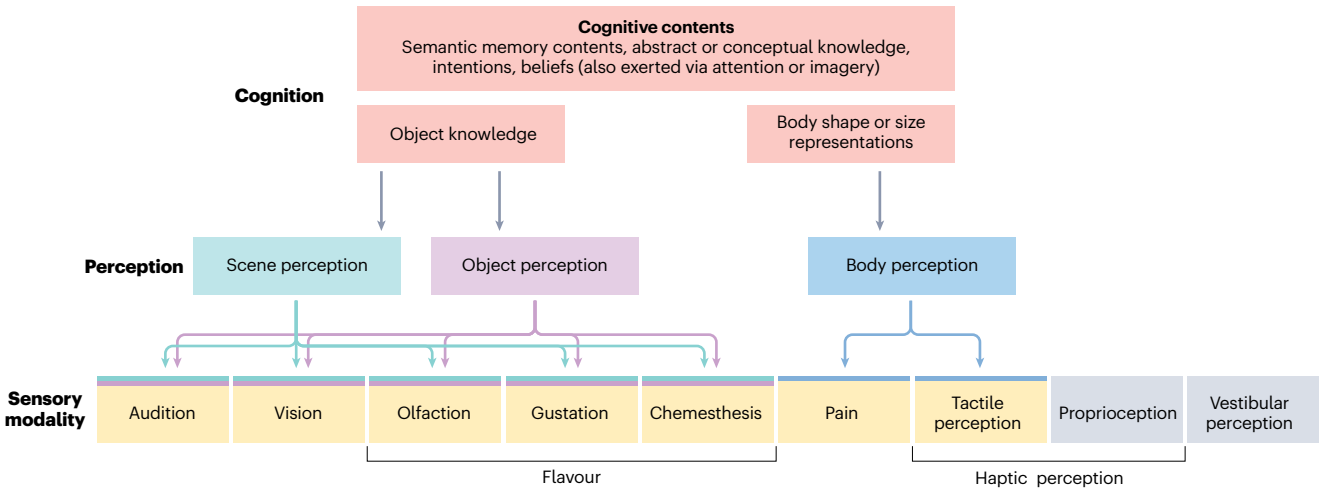


Fig. 4 | Influences of cognition on perception across the senses. Cognition is defined here as a higher cognitive content, such as semantic memory content, abstract or conceptual knowledge, or a belief or intention, that can also be exerted via endogenous attention or mental imagery that carries cognitive information. Cognition (red boxes) can influence scene and object perception (green and purple boxes) in audition, vision, pain and haptic perception (arising from a combination of tactile perception and proprioception), olfaction and gustation (with flavour arising from both smell and taste). Cognition also influences tactile perception via changes in body representations (blue box). By contrast, proprioception and vestibular processing (grey) are largely unaffected by cognition.

high clinical and practical relevance and is accordingly well funded. Thus, a lot of evidence for cognitive penetrability has accumulated in this field. A lack of evidence for cognitive penetrability in vestibular processing, proprioception and chemesthesis might therefore partly reflect the low volume of research in these senses. In a complex topic such as cognitive penetrability, the quantity of research matters in weighing the evidence.

With this caveat in mind, we discuss possible reasons for the observed differences both across the senses and based on the type of influence.

Differences across senses

The answer to whether perception is cognitively penetrable depends heavily on which perceptual experience is being considered (Fig. 4). There are likely evolutionary reasons for these differences. Susceptibility of vision, audition, olfaction and parts of somatosensory perception to cognitive influences might be highly adaptive. Sensory information from these channels is complex, manifold, and potentially noisy and ambiguous. In such conditions, the organism might need to integrate prior experience, contextual information and memory content to create a percept that provides the best possible representation of the outside world. For example, the olfactory system can theoretically discriminate a much larger number of odours than could possibly be functionally relevant and the brain will classify these sensory experiences into 'smell objects' on the basis of associations with a shared source[208,232,233]. Similarly, in natural viewing and hearing conditions (that is, not under the controlled conditions of a laboratory), visual and auditory input is complex and often ambiguous (owing to factors such as occlusion and masking) and needs to be 'clarified' by contextual information and previous expectations[75,234]. In touch, sensory processing is facilitated by temporal expectations[235,236]. Taking prior knowledge and context into account reduces the complexity and processing load of sensory information and makes this information predictable for the brain. Predictions are a key ingredient for fast, accurate and resource-efficient processing to create a percept out of an overwhelming amount of sensory information[234,237].

The fact that the vestibular system and proprioception seem to be mostly impenetrable by cognition might be related to their fundamental importance for conveying information not about the environment, as in most other senses, but about the position of the head and body in space, which is crucial for the ability to successfully adapt to the external environment. Penetrability to cognitive influences might be maladaptive in these senses because the grounding of one's body in space needs to remain stable and should not be highly dependent on context. Instead of a direct influence, the influence of vision on the vestibular system (such as for balance control) and on proprioception might provide an indirect way by which cognition can influence these bodily senses. For example, visual and vestibular signals are constantly integrated to calibrate one's head position in space with respect to the eyes[238] and seeing a rubber hand is sufficient to induce proprioceptive drift[147]. These changes reflect a multisensory rather than cognitive influence, with the visual channel of vestibular and proprioceptive sensing being cognitively penetrable.

The relative lack of cognitive penetrability of chemesthesis and gustation might be due to their lack of dimensionality, which makes these sensory qualities very distinguishable and therefore less prone to contextual adjustment (apart from their hedonic evaluation). However, evidence regarding cognitive penetrability of chemesthesis and gustation, especially neuroimaging evidence, remains incomplete. Lack of dimensionality fails to explain why pain, a fundamental physiological response to physical body damage of low dimensionality, is so clearly cognitively penetrable. A possible explanation could be that cognitive penetration of pain might be a survival mechanism that enables at least temporary suppression of the pain response to ensure fundamental survival such as reaching a safe space or getting enough food despite injury or illness.

Cognitive penetrability of somatosensation seems to depend on the extent to which information from another sense and prior knowledge is integrated. In haptic perception, in which tactile and proprioceptive signals are integrated, cognitive knowledge about the touched objects affects haptic perception. Similarly, cognitive knowledge about body shape influences spatial perception of touch. On the other hand, the integration of vision and proprioception in the rubber hand illusion seems to be resistant to cognitive influences, potentially because proprioception, like the vestibular system, provides basic information about the body rather than the environment.

Types of influence

In addition to distinguishing types of perceptual experience by sensory modality, it might be equally important to distinguish types of influence that penetrate perceptual experiences — whether they are cognitive, emotional, or multisensory and whether they are direct or indirect influences. Although some senses might not be penetrable by higher cognitive contents, by their nature, they are sometimes heavily influenced by information from other sensory modalities[239]. For example, vestibular, proprioceptive, tactile and gustatory perception are highly influenced by visual signals, and vision is often cognitively penetrable. Thus, cognitive factors might assert an indirect influence on some sensory modalities via multisensory interactions. A similar argument can be made about attention and imagery: although not every cognitive factor can influence perception directly, it might do so indirectly by shifting feature or object attention or via an intermediate process of mental imagery[4], including across sensory modalities.

Another interesting idea that emerges when considering multiple sensory modalities is that hedonic evaluation (for example, pleasantness or unpleasantness) of sensory information is intricately connected to its perceptual experience, for example, in affective touch[140] and olfactory perception[240]. In these modalities, the hedonic evaluation of the perceptual experience is an essential part of 'what it is like' to have this experience. In these instances, the theoretical distinction between perceptual experience itself and judgement of the hedonic quality of the percept is not reflected in neural sensory processing and the functional and anatomical organization of the brain. Furthermore, one could conceptualize hedonic evaluation as a cognitive process that is ingrained in perceptual experience in these modalities, which would speak strongly in favour of cognitive penetration. Once again, the debate of cognitive penetrability strongly hinges on what counts as cognition and cognitive factors[1,5]. What counts as cognitive determines whether, for example, prior object knowledge that influences haptic perception, or the expectation that redness changes the sweetness of a fruit, are instances of cognitive penetrability. Likewise, the abstract knowledge about the intentions of a person stroking one's arm could be considered cognitive, emotional or judgemental, with differing implications for cognitive penetrability.

Although theoretical debates make clear distinctions between words like 'cognition', 'evaluation', 'emotion' and 'perception', these distinctions map poorly onto brain functioning. Given the evidence that the brain is heavily interconnected, and constant, fast and recurrent processing happens between and across a huge variety of brain regions, it seems difficult (and potentially even maladaptive and inefficient) to draw strict boundaries between these different processes. It is more likely that many of these brain processes happen concurrently and in parallel. For instance, seeing the redness of a fruit might activate the concept of sweetness, thereby biasing gustatory perception towards higher sweetness.

From the reviewed neural evidence, it is clear that every sensory modality engages a wide network of brain areas that interact closely with each other to create a conscious perceptual experience. It is highly unlikely that none of these areas are influenced by brain areas and processing streams that carry some kind of cognitive information. For example, the vestibular system, which seems comparably unaffected by cognitive influence, is nonetheless heavily cross-modally interconnected and could indirectly be influenced by, for example, visual object knowledge. Thus, our conclusion is that, although the extent to which cognition influences perception differs across the different senses, the postulation of 'informationally encapsulated' perceptual modules fails to hold true for any sensory modality. Instead, the reviewed evidence supports the notion that cognitive penetration of perception does indeed exist in the majority of sensory modalities, including vision, audition, olfaction, pain, haptic and tactile perception.

Summary and future directions

In this Review, we considered different sensory modalities to extend the debate on the cognitive penetrability of perception. First, we showed that some senses are more penetrable and some are less penetrable by cognition, and others seem at best indirectly penetrable through cross-modal influences from penetrable senses. Thus, the question of whether cognition penetrates perception needs to be differentiated by sensory modality. Second, there are many different types of influence on perception (including cross-modal, evaluative, direct and indirect), each of which carries some cognitive information, albeit to different extents. Thus, the question of whether cognition penetrates perception depends very much on what is regarded as cognition. This distinction is a theoretical one rather than one that reflects how the brain operates, as supported by the reviewed neural evidence. 'Informationally encapsulated' perceptual modules are a rather implausible model for thinking about how perception unfolds. Instead, we conclude that the majority of perceptual experience is a result of rich interactions between cognitive, sensory and multisensory processes.

In future research, we recommend that experimentalists in all sensory modalities address the question of cognitive penetrability of perception more directly, studying influences from clearly high-level cognitive states and avoiding confounding factors when measuring perception. We recommend carefully choosing experimental designs and measures that enable the researcher to distinguish perceptual experience from response bias (for example, by combining measures of d', thresholds, reaction times and confidence ratings; Box 1). Furthermore, as mentioned above, the reviewed evidence might itself be biased by the number of studies that addressed the question of cognitive penetrability in each sensory modality. Thus, for a more complete picture of cognitive penetrability of perception, we recommend increasing the research effort, particularly in touch, haptic perception, proprioception, vestibular processing, gustation and chemesthesis. Illuminating how cognition can influence those senses could potentially be of clinical relevance, for example, in balance control, body perception and loss of flavour perception. For example, a better understanding of cognitive penetrability could help to determine whether cognition could influence balance training in patients with vestibular disorders, body image in patients with eating disorders or partial rehabilitation of flavour loss.

We also recommend that theorists draw careful distinctions among potential penetrating factors — especially with respect to different aspects of cognition, evaluation and emotion — and clearly define any further penetrating factors. Additionally, we strongly recommend

the incorporation of neuroscientific evidence into models of how the brain plausibly creates one's perception of the world.

Overall, the reviewed evidence suggests that cognitive and perceptual brain processes are heavily intertwined. The brain provides a functional representation of the world that enables survival and is nevertheless not entirely determinable by one's subjective thoughts. However, the exact intricacies of the interaction between cognition and perception still require further careful investigation.

Published online: 18 November 2024

References

1. Cermeño-Aínsa, S. The cognitive penetrability of perception: a blocked debate and a tentative solution. *Conscious. Cogn.* **77**, 102838 (2020).
2. Firestone, C. & Scholl, B. J. Cognition does not affect perception: evaluating the evidence for 'top-down' effects. *Behav. Brain Sci.* **39**, e229 (2016).
3. Lupyan, G. Cognitive penetrability of perception in the age of prediction: predictive systems are penetrable systems. *Rev. Philos. Psychol.* **6**, 547–569 (2015).
4. Macpherson, F. Cognitive penetration of colour experience: rethinking the issue in light of an indirect mechanism. *Philos. Phenomenol. Res.* **84**, 24–62 (2012).
5. Newen, A. & Vetter, P. Why cognitive penetration of our perceptual experience is still the most plausible account. *Conscious. Cogn.* **47**, 26–37 (2017).
6. O'Callaghan, C., Kveraga, K., Shine, J. M., Adams, R. B. & Bar, M. Predictions penetrate perception: converging insights from brain, behaviour and disorder. *Conscious. Cogn.* **47**, 63–74 (2017).
7. Raftopoulos, A. The cognitive impenetrability of the content of early vision is a necessary and sufficient condition for purely nonconceptual content. *Philos. Psychol.* **27**, 601–620 (2014).
8. Stokes, D. *Thinking and Perceiving: on the Malleability of the Mind* (Routledge, 2021).
9. Vetter, P. & Newen, A. Varieties of cognitive penetration in visual perception. *Conscious. Cogn.* **27**, 62–75 (2014).
10. Block, N. *The Border between Seeing and Thinking* (Oxford University Press, 2023).
11. Fodor, J. A. *The Modularity of Mind: An Essay on Faculty Psychology* (MIT Press, 1983).
12. Pylyshyn, Z. Is vision continuous with cognition? The case for cognitive impenetrability of visual perception. *Behav. Brain Sci.* **22**, 341–365 (1999).
13. Zeki, S. A century of cerebral achromatopsia. *Brain* **113**, 1721–1777 (1990).
14. Lueck, C. J. et al. The colour centre in the cerebral cortex of man. *Nature* **340**, 386–389 (1989).
15. Cristofori, I., Cohen-Zimerman, S. & Grafman, J. Executive functions. *Handb. Clin. Neurol.* **163**, 197–219 (2019).
16. Lamme, V. A. F. Why visual attention and awareness are different. *Trends Cogn. Sci.* **7**, 12–18 (2003).
17. Clark, A. Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behav. Brain Sci.* **36**, 181–204 (2013).
18. Teufel, C. & Nanay, B. How to (and how not to) think about top-down influences on visual perception. *Conscious. Cogn.* **47**, 17–25 (2017).
19. Markov, N. T. et al. Cortical high-density counterstream architectures. *Science* **342**, 1238406 (2013).
20. Gilbert, C. D. & Li, W. Top-down influences on visual processing. *Nat. Rev. Neurosci.* **14**, 350–363 (2013).
This paper is a review of different types of top-down influence in vision and how cortical feedback pathways exert these influences.
21. Hochstein, S. & Ahissar, M. View from the top: hierarchies and reverse hierarchies in the visual system. *Neuron* **36**, 791–804 (2002).
22. Kietzmann, T. C. et al. Recurrence is required to capture the representational dynamics of the human visual system. *Proc. Natl Acad. Sci. USA* **116**, 21854–21863 (2019).
23. Lamme, V. A. & Roelfsema, P. R. The distinct modes of vision offered by feedforward and recurrent processing. *Trends Neurosci.* **23**, 571–579 (2000).
24. Siu, C., Balsor, J., Merlin, S., Federer, F. & Angelucci, A. A direct interareal feedback-to-feedforward circuit in primate visual cortex. *Nat. Commun.* **12**, 4911 (2021).
25. Gregory, R. L. *Seeing Through Illusions* (Oxford University Press, 2009).
26. Cavanagh, P. et al. The architecture of object-based attention. *Psychon. Bull. Rev.* **30**, 1643–1667 (2023).
27. Carrasco, M. & Barbot, A. Spatial attention alters visual appearance. *Curr. Opin. Psychol.* **29**, 56–64 (2019).
28. Pearson, J. The human imagination: the cognitive neuroscience of visual mental imagery. *Nat. Rev. Neurosci.* **20**, 624–634 (2019).
29. Girshick, A. R., Landy, M. S. & Simoncelli, E. P. Cardinal rules: visual orientation perception reflects knowledge of environmental statistics. *Nat. Neurosci.* **14**, 926–932 (2011).
30. Badde, S. & Heed, T. The hands' default location guides tactile spatial selectivity. *Proc. Natl Acad. Sci. USA* **120**, e2209680120 (2023).
31. Badde, S., Röder, B. & Heed, T. Feeling a touch to the hand on the foot. *Curr. Biol.* **29**, 1491–1497.e4 (2019).
32. Green, C. S., Banai, K., Lu, Z. & Bavelier, D. In: *Stevens' Handbook of Experimental Psychology and Cognitive Neuroscience* (ed. Wixted, J. T.) 1–47 (Wiley, 2018).
33. Phelps, E. A. Emotion and cognition: insights from studies of the human amygdala. *Annu. Rev. Psychol.* **57**, 27–53 (2006).
34. Salmela, M. Can emotion be modelled on perception? *Dialectica* **65**, 1–29 (2011).
35. Niedenthal, P. M. & Wood, A. Does emotion influence visual perception? Depends on how you look at it. *Cogn. Emot.* **33**, 77–84 (2019).
36. Choi, I., Lee, J.-Y. & Lee, S.-H. Bottom-up and top-down modulation of multisensory integration. *Curr. Opin. Neurobiol.* **52**, 115–122 (2018).
37. Murray, M. M. & Wallace, M. T. *The Neural Bases of Multisensory Processes* (CRC Press/Taylor & Francis, 2012).
38. Lupyan, G. & Spivey, M. J. Making the invisible visible: verbal but not visual cues enhance visual detection. *PLoS ONE* **5**, e11452 (2010).
39. Lupyan, G. & Ward, E. J. Language can boost otherwise unseen objects into visual awareness. *Proc. Natl Acad. Sci. USA* **110**, 14196–14201 (2013).
40. Chen, Y.-C. & Spence, C. When hearing the bark helps to identify the dog: semantically-congruent sounds modulate the identification of masked pictures. *Cognition* **114**, 389–404 (2010).
41. Chen, Y.-C. & Spence, C. Crossmodal semantic priming by naturalistic sounds and spoken words enhances visual sensitivity. *J. Exp. Psychol. Hum. Percept. Perform.* **37**, 1554–1568 (2011).
42. Teufel, C., Dakin, S. C. & Fletcher, P. C. Prior object-knowledge sharpens properties of early visual feature-detectors. *Sci. Rep.* **8**, 10853 (2018).
43. Samaha, J., Boutonnet, B., Postle, B. R. & Lupyan, G. Effects of meaningfulness on perception: alpha-band oscillations carry perceptual expectations and influence early visual responses. *Sci. Rep.* **8**, 6606 (2018).
44. Berger, C. C. & Ehrsson, H. H. The content of imagined sounds changes visual motion perception in the cross-bounce illusion. *Sci. Rep.* **7**, 40123 (2017).
45. Yuval-Greenberg, S. & Heeger, D. J. Continuous flash suppression modulates cortical activity in early visual cortex. *J. Neurosci.* **33**, 9635–9643 (2013).
46. Mathôt, S. Tuning the senses: how the pupil shapes vision at the earliest stage. *Annu. Rev. Vis. Sci.* **6**, 433–451 (2020).
47. Binda, P., Pereverzeva, M. & Murray, S. O. Pupil constrictions to photographs of the sun. *J. Vis.* **13**, 8 (2013).
48. Castellotti, S., Conti, M., Feitosa-Santana, C. & Del Viva, M. M. Pupillary response to representations of light in paintings. *J. Vis.* **20**, 14 (2020).
49. Naber, M. & Nakayama, K. Pupil responses to high-level image content. *J. Vis.* **13**, 7 (2013).
50. Mathôt, S., Grainger, J. & Strijkers, K. Pupillary responses to words that convey a sense of brightness or darkness. *Psychol. Sci.* **28**, 1116–1124 (2017).
51. Laeng, B. & Sulutvedt, U. The eye pupil adjusts to imaginary light. *Psychol. Sci.* **25**, 188–197 (2014).
52. Hustá, C., Dalmaijer, E., Belopolsky, A. & Mathôt, S. The pupillary light response reflects visual working memory content. *J. Exp. Psychol. Hum. Percept. Perform.* **45**, 1522–1528 (2019).
53. Xie, W. & Zhang, W. Pupillary evidence reveals the influence of conceptual association on brightness perception. *Psychon. Bull. Rev.* **30**, 1388–1395 (2023).
54. Peelen, M. V. & Downing, P. E. Testing cognitive theories with multivariate pattern analysis of neuroimaging data. *Nat. Hum. Behav.* **7**, 1430–1441 (2023).
55. Kay, K., Bonnen, K., Denison, R. N., Arcaro, M. J. & Barack, D. L. Tasks and their role in visual neuroscience. *Neuron* **111**, 1697–1713 (2023).
This paper provides an overview of the diverse ways in which tasks influence visual processing.
56. Uithol, S., Bryant, K. L., Toni, I. & Mars, R. B. The anticipatory and task-driven nature of visual perception. *Cereb. Cortex* **31**, 5354–5362 (2021).
57. Harel, A., Kravitz, D. J. & Baker, C. I. Task context impacts visual object processing differentially across the cortex. *Proc. Natl Acad. Sci. USA* **111**, E962–E971 (2014).
58. Çukur, T., Nishimoto, S., Huth, A. G. & Gallant, J. L. Attention during natural vision warps semantic representation across the human brain. *Nat. Neurosci.* **16**, 763–770 (2013).
59. Kay, K. & Yeatman, J. D. Bottom-up and top-down computations in word- and face-selective cortex. *eLife* **6**, e22341 (2017).
60. White, A. L., Kay, K., Tang, K. A. & Yeatman, J. D. Engaging in word recognition elicits highly specific modulations in visual cortex. *Curr. Biol.* **33**, 1308–1320.e5 (2023).
61. Hebart, M. N., Bankson, B. B., Harel, A., Baker, C. I. & Cichy, R. M. The representational dynamics of task and object processing in humans. *eLife* **7**, e32816 (2018).
62. Breedlove, J. L., St-Yves, G., Olman, C. A. & Naselaris, T. Generative feedback explains distinct brain activity codes for seen and mental images. *Curr. Biol.* **30**, 2211–2224.e6 (2020).
63. Bannert, M. M. & Bartels, A. Decoding the yellow of a gray banana. *Curr. Biol.* **23**, 2268–2272 (2013).
64. Kok, P., Jehee, J. F. M. & de Lange, F. P. Less is more: expectation sharpens representations in the primary visual cortex. *Neuron* **75**, 265–270 (2012).
65. Favila, S. E., Kuhl, B. A. & Winawer, J. Perception and memory have distinct spatial tuning properties in human visual cortex. *Nat. Commun.* **13**, 5864 (2022).
66. Yan, C., de Lange, F. P. & Richter, D. Conceptual associations generate sensory predictions. *J. Neurosci.* **43**, 3733–3742 (2023).
67. Harrison, S. A. & Tong, F. Decoding reveals the contents of visual working memory in early visual areas. *Nature* **458**, 632–635 (2009).
68. Rademaker, R. L., Chunharas, C. & Serences, J. T. Coexisting representations of sensory and mnemonic information in human visual cortex. *Nat. Neurosci.* **22**, 1336–1344 (2019).
69. Gutteling, T. P. et al. Action preparation shapes processing in early visual cortex. *J. Neurosci.* **35**, 6472–6480 (2015).

70. Yon, D., Gilbert, S. J., de Lange, F. P. & Press, C. Action sharpens sensory representations of expected outcomes. *Nat. Commun.* **9**, 4288 (2018).
71. Monaco, S., Gallivan, J. P., Figley, T. D., Singhal, A. & Culham, J. C. Recruitment of foveal retinotopic cortex during haptic exploration of shapes and actions in the dark. *J. Neurosci.* **37**, 11572–11591 (2017).
72. de Haas, B., Schwarzkopf, D. S., Urner, M. & Rees, G. Auditory modulation of visual stimulus encoding in human retinotopic cortex. *NeuroImage* **70**, 258–267 (2013).
73. Vetter, P., Smith, F. W. & Muckli, L. Decoding sound and imagery content in early visual cortex. *Curr. Biol.* **24**, 1256–1262 (2014).
74. Petro, L. S., Vizioli, L. & Muckli, L. Contributions of cortical feedback to sensory processing in primary visual cortex. *Front. Psychol.* **5**, 1223 (2014).
75. Wyatte, D., Jilk, D. J. & O'Reilly, R. C. Early recurrent feedback facilitates visual object recognition under challenging conditions. *Front. Psychol.* **5**, 674 (2014).
76. Bashford, J. A. & Warren, R. M. Multiple phonemic restorations follow the rules for auditory induction. *Percept. Psychophys.* **42**, 114–121 (1987).
77. Samuel, A. Phoneme restoration. *Lang. Cogn. Process.* **11**, 647–654 (1996).
78. Warren, R. M., Obusek, C. J. & Ackroff, J. M. Auditory induction: perceptual synthesis of absent sounds. *Science* **176**, 1149–1151 (1972).
79. Ciocca, V. & Bregman, A. S. Perceived continuity of gliding and steady-state tones through interrupting noise. *Percept. Psychophys.* **42**, 476–484 (1987).
80. Lyzenga, J., Carlyon, R. P. & Moore, B. C. J. Dynamic aspects of the continuity illusion: perception of level and of the depth, rate, and phase of modulation. *Hear. Res.* **210**, 30–41 (2005).
81. Cervantes Constantino, F. & Simon, J. Z. Dynamic cortical representations of perceptual filling-in for missing acoustic rhythm. *Sci. Rep.* **7**, 17536 (2017).
82. Riecke, L. et al. Recalibration of the auditory continuity illusion: sensory and decisional effects. *Hear. Res.* **277**, 152–162 (2011).
83. Mattys, S. L., Davis, M. H., Bradlow, A. R. & Scott, S. K. Speech recognition in adverse conditions: a review. *Lang. Cogn. Process.* **27**, 953–978 (2012).
This paper is a review of the role of prediction, at all levels, in perception of speech.
84. Gwilliams, L., Linzen, T., Poeppel, D. & Marantz, A. In spoken word recognition, the future predicts the past. *J. Neurosci.* **38**, 7585–7599 (2018).
85. Ganong, W. F. Phonetic categorization in auditory word perception. *J. Exp. Psychol. Hum. Percept. Perform.* **6**, 110–125 (1980).
86. Freyman, R. L., Morse-Fortier, C. & Griffin, A. M. Temporal effects in priming of masked and degraded speech. *J. Acoust. Soc. Am.* **138**, 1418–1427 (2015).
87. Sheldon, S., Pichora-Fuller, M. K. & Schneider, B. A. Priming and sentence context support listening to noise-vocoded speech by younger and older adults. *J. Acoust. Soc. Am.* **123**, 489–499 (2008).
88. Guediche, S., Reilly, M., Santiago, C., Laurent, P. & Blumstein, S. E. An fMRI study investigating effects of conceptually related sentences on the perception of degraded speech. *Cortex* **79**, 57–74 (2016).
89. Cummings, A. et al. Auditory semantic networks for words and natural sounds. *Brain Res.* **1115**, 92–107 (2006).
90. Orgs, G., Lange, K., Dombrowski, J.-H. & Heil, M. Conceptual priming for environmental sounds and words: an ERP study. *Brain Cogn.* **62**, 267–272 (2006).
91. Frey, A., Aramaki, M. & Besson, M. Conceptual priming for realistic auditory scenes and for auditory words. *Brain Cogn.* **84**, 141–152 (2014).
92. Maye, J., Aslin, R. N. & Tanenhaus, M. K. The weckud wetch of the wast: lexical adaptation to a novel accent. *Cogn. Sci.* **32**, 543–562 (2008).
93. Norris, D. Perceptual learning in speech. *Cognit. Psychol.* **47**, 204–238 (2003).
94. Bradlow, A. R. & Bent, T. Perceptual adaptation to non-native speech. *Cognition* **106**, 707–729 (2008).
95. Reinisch, E. & Holt, L. L. Lexically guided phonetic retuning of foreign-accented speech and its generalization. *J. Exp. Psychol. Hum. Percept. Perform.* **40**, 539–555 (2014).
96. Xie, X. & Myers, E. B. Learning a talker or learning an accent: acoustic similarity constrains generalization of foreign accent adaptation to new talkers. *J. Mem. Lang.* **97**, 30–46 (2017).
97. Trude, A. M. & Brown-Schmidt, S. Talker-specific perceptual adaptation during online speech perception. *Lang. Cogn. Process.* **27**, 979–1001 (2012).
98. Agus, T. R. & Pressnitzer, D. Repetition detection and rapid auditory learning for stochastic tone clouds. *J. Acoust. Soc. Am.* **150**, 1735–1749 (2021).
99. Herrmann, B., Araz, K. & Johnsrude, I. S. Sustained neural activity correlates with rapid perceptual learning of auditory patterns. *NeuroImage* **238**, 118238 (2021).
This paper reports evidence for direct changes in neural coding acoustic inputs based on recent context.
100. Agus, T. R. & Pressnitzer, D. The detection of repetitions in noise before and after perceptual learning. *J. Acoust. Soc. Am.* **134**, 464–473 (2013).
101. Ringer, H., Schröger, E. & Grimm, S. Perceptual learning of random acoustic patterns: impact of temporal regularity and attention. *Eur. J. Neurosci.* **57**, 2112–2135 (2023).
102. Bianco, R. et al. Long-term implicit memory for sequential auditory patterns in humans. *eLife* **9**, e56073 (2020).
103. Heinrich, A., Carlyon, R. P., Davis, M. H. & Johnsrude, I. S. Illusory vowels resulting from perceptual continuity: a functional magnetic resonance imaging study. *J. Cogn. Neurosci.* **20**, 1737–1752 (2008).
104. Heinrich, A., Carlyon, R. P., Davis, M. H. & Johnsrude, I. S. The continuity illusion does not depend on attentional state: fMRI evidence from illusory vowels. *J. Cogn. Neurosci.* **23**, 2675–2689 (2011).
105. Shahin, A. J., Bishop, C. W. & Miller, L. M. Neural mechanisms for illusory filling-in of degraded speech. *NeuroImage* **44**, 1133–1143 (2009).
106. Riecke, L., Esposito, F., Bonte, M. & Formisano, E. Hearing illusory sounds in noise: the timing of sensory-perceptual transformations in auditory cortex. *Neuron* **64**, 550–561 (2009).
107. Hannemann, R., Obleser, J. & Eulitz, C. Top-down knowledge supports the retrieval of lexical information from degraded speech. *Brain Res.* **1153**, 134–143 (2007).
108. Baltzell, L. S., Srinivasan, R. & Richards, V. M. The effect of prior knowledge and intelligibility on the cortical entrainment response to speech. *J. Neurophysiol.* **118**, 3144–3151 (2017).
This paper reports neural evidence that previous inputs alter coding of subsequent speech.
109. Banellis, L., Sokoliuk, R., Wild, C. J., Bowman, H. & Cruse, D. Event-related potentials reflect prediction errors and pop-out during comprehension of degraded speech. *Neurosci. Conscious.* **2020**, niaa022 (2020).
110. Yi, H. G., Leonard, M. K. & Chang, E. F. The encoding of speech sounds in the superior temporal gyrus. *Neuron* **102**, 1096–1110 (2019).
111. Sohoglu, E., Peelle, J. E., Carlyon, R. P. & Davis, M. H. Predictive top-down integration of prior knowledge during speech perception. *J. Neurosci.* **32**, 8443–8453 (2012).
112. Leonard, M. K., Baud, M. O., Sjerps, M. J. & Chang, E. F. Perceptual restoration of masked speech in human cortex. *Nat. Commun.* **7**, 13619 (2016).
113. Lim, S.-J., Fiez, J. A. & Holt, L. L. Role of the striatum in incidental learning of sound categories. *Proc. Natl Acad. Sci. USA* **116**, 4671–4680 (2019).
114. Lim, S. & Holt, L. L. Learning foreign sounds in an alien world: videogame training improves non-native speech categorization. *Cogn. Sci.* **35**, 1390–1405 (2011).
115. Ley, A. et al. Learning of new sound categories shapes neural response patterns in human auditory cortex. *J. Neurosci.* **32**, 13273–13280 (2012).
116. Fritz, J. B., Elhilali, M., David, S. V. & Shamma, S. A. Auditory attention — focusing the searchlight on sound. *Curr. Opin. Neurobiol.* **17**, 437–455 (2007).
117. Maddox, R. K. & Shinn-Cunningham, B. G. Influence of task-relevant and task-irrelevant feature continuity on selective auditory attention. *J. Assoc. Res. Otolaryngol.* **13**, 119–129 (2012).
118. Noyce, A. L., Cestero, N., Michalka, S. W., Shinn-Cunningham, B. G. & Somers, D. C. Sensory-biased and multiple-demand processing in human lateral frontal cortex. *J. Neurosci.* **37**, 8755–8766 (2017).
119. Larson, E. & Lee, A. K. C. Switching auditory attention using spatial and non-spatial features recruits different cortical networks. *NeuroImage* **84**, 681–687 (2014).
120. Michalka, S. W., Rosen, M. L., Kong, L., Shinn-Cunningham, B. G. & Somers, D. C. Auditory spatial coding flexibly recruits anterior, but not posterior, visuotopic parietal cortex. *Cereb. Cortex* **26**, 1302–1308 (2016).
121. Hill, K. T. & Miller, L. M. Auditory attentional control and selection during cocktail party listening. *Cereb. Cortex* **20**, 583–590 (2010).
122. Michalka, S. W., Kong, L., Rosen, M. L., Shinn-Cunningham, B. G. & Somers, D. C. Short-term memory for space and time flexibly recruit complementary sensory-biased frontal lobe attention networks. *Neuron* **87**, 882–892 (2015).
123. Lee, A. K. C. et al. Auditory selective attention reveals preparatory activity in different cortical regions for selection based on source location and source pitch. *Front. Neurosci.* **6**, 190 (2013).
124. Anourova, I. et al. Evidence for dissociation of spatial and nonspatial auditory information processing. *NeuroImage* **14**, 1268–1277 (2001).
125. Anurova, I. et al. Differences between auditory evoked responses recorded during spatial and nonspatial working memory tasks. *NeuroImage* **20**, 1181–1192 (2003).
126. Leavitt, V. M., Molholm, S., Gomez-Ramirez, M. & Foxe, J. J. "What" and "where" in auditory sensory processing: a high-density electrical mapping study of distinct neural processes underlying sound object recognition and sound localization. *Front. Integr. Neurosci.* **5**, 23 (2011).
127. Fleming, J. T., Njoroge, J. M., Noyce, A. L., Perrachione, T. K. & Shinn-Cunningham, B. G. Sensory modality and information domain contribute jointly to dual-task interference between working memory and perceptual processing. *Imaging Neurosci.* **2**, 1–22 (2024).
128. Shinn-Cunningham, B., Best, V. & Lee, A. K. C. In: *The Auditory System at the Cocktail Party* (eds Middlebrooks, J. C., Simon, J. Z., Popper, A. N. & Fay, R. R.) 60, 7–40 (Springer International Publishing, 2017).
129. Delhaye, B. P., Long, K. H. & Bensmaia, S. J. Neural basis of touch and proprioception in primate cortex. *Compr. Physiol.* **8**, 1575–1602 (2018).
130. Badde, S., Navarro, K. T. & Landy, M. S. Modality-specific attention attenuates visual-tactile integration and recalibration effects by reducing prior expectations of a common source for vision and touch. *Cognition* **197**, 104170 (2020).
131. Samad, M. & Shams, L. Visual–somatotopic interactions in spatial perception. *NeuroReport* **27**, 180–185 (2016).
132. Van Beers, R. J., Sittig, A. C. & Van Der Gon Denier, J. J. How humans combine simultaneous proprioceptive and visual position information. *Exp. Brain Res.* **111**, 253–261 (1996).
133. Goldreich, D. A Bayesian perceptual model replicates the cutaneous rabbit and other tactile spatiotemporal illusions. *PLoS ONE* **2**, e333 (2007).
134. Tajadura-Jiménez, A. et al. Action sounds recalibrate perceived tactile distance. *Curr. Biol.* **22**, R516–R517 (2012).
135. Miller, L. E., Cawley-Bennett, A., Longo, M. R. & Saygin, A. P. The recalibration of tactile perception during tool use is body-part specific. *Exp. Brain Res.* **235**, 2917–2926 (2017).
136. Markmann, M. et al. Hypnotic suggestions cognitively penetrate tactile perception through top-down modulation of semantic contents. *Sci. Rep.* **13**, 6578 (2023).
This paper is one of very few that directly probes cognitive penetrability of tactile perception, here by means of hypnotic suggestion.

137. Taylor-Clarke, M., Jacobsen, P. & Haggard, P. Keeping the world a constant size: object constancy in human touch. *Nat. Neurosci.* **7**, 219–220 (2004).
138. Kennett, S., Taylor-Clarke, M. & Haggard, P. Noninformative vision improves the spatial resolution of touch in humans. *Curr. Biol.* **11**, 1188–1191 (2001).
139. Haggard, P., Christakou, A. & Serino, A. Viewing the body modulates tactile receptive fields. *Exp. Brain Res.* **180**, 187–193 (2007).
140. McGlone, F., Wessberg, J. & Olausson, H. Discriminative and affective touch: sensing and feeling. *Neuron* **82**, 737–755 (2014).
141. McCabe, C., Rolls, E. T., Bilderbeck, A. & McGlone, F. Cognitive influences on the affective representation of touch and the sight of touch in the human brain. *Soc. Cogn. Affect. Neurosci.* **3**, 97–108 (2008).
142. Ravaja, N., Harjunen, V., Ahmed, I., Jacucci, G. & Spapé, M. M. Feeling touched: emotional modulation of somatosensory potentials to interpersonal touch. *Sci. Rep.* **7**, 40504 (2017).
143. Gazzola, V. et al. Primary somatosensory cortex discriminates affective significance in social touch. *Proc. Natl Acad. Sci. USA* **109**, E1657–E1666 (2012).
144. Case, L. K. et al. Encoding of touch intensity but not pleasantness in human primary somatosensory cortex. *J. Neurosci.* **36**, 5850–5860 (2016).
145. Botvinick, M. & Cohen, J. Rubber hands 'feel' touch that eyes see. *Nature* **391**, 756 (1998).
146. Holle, H., McLatchie, N., Maurer, S. & Ward, J. Proprioceptive drift without illusions of ownership for rotated hands in the "rubber hand illusion" paradigm. *Cogn. Neurosci.* **2**, 171–178 (2011).
147. Rohde, M., Di Luca, M. & Ernst, M. O. The rubber hand illusion: feeling of ownership and proprioceptive drift do not go hand in hand. *PLoS ONE* **6**, e21659 (2011).
148. Dempsey-Jones, H. & Kritikos, A. Higher-order cognitive factors affect subjective but not proprioceptive aspects of self-representation in the rubber hand illusion. *Conscious. Cogn.* **26**, 74–89 (2014).
149. Brunyé, T. T. et al. The fabric of thought: priming tactile properties during reading influences direct tactile perception. *Cogn. Sci.* **36**, 1449–1467 (2012).
150. Metzger, A. & Drewing, K. Memory influences haptic perception of softness. *Sci. Rep.* **9**, 14383 (2019).
151. Klatzky, R. L. & Lederman, S. J. Identifying objects from a haptic glance. *Percept. Psychophys.* **57**, 1111–1123 (1995).
152. Deshpande, G., Hu, X., Lacey, S., Stilla, R. & Sathian, K. Object familiarity modulates effective connectivity during haptic shape perception. *NeuroImage* **49**, 1991–2000 (2010).
153. Kaptchuk, T. J. & Miller, F. G. Placebo effects in medicine. *N. Engl. J. Med.* **373**, 8–9 (2015).
154. Ellingsen, D.-M. et al. Placebo improves pleasure and pain through opposite modulation of sensory processing. *Proc. Natl Acad. Sci. USA* **110**, 17993–17998 (2013).
155. Wager, T. D. et al. Placebo-induced changes in fMRI in the anticipation and experience of pain. *Science* **303**, 1162–1167 (2004).
156. Zunhammer, M. et al. Meta-analysis of neural systems underlying placebo analgesia from individual participant fMRI data. *Nat. Commun.* **12**, 1391 (2021).
157. Wager, T. D. & Atlas, L. Y. The neuroscience of placebo effects: connecting context, learning and health. *Nat. Rev. Neurosci.* **16**, 403–418 (2015).
This review focuses on physiological correlates of placebo effects as well as the cognitive and non-cognitive processes behind these effects.
158. Fetsch, C. R., Turner, A. H., DeAngelis, G. C. & Angelaki, D. E. Dynamic reweighting of visual and vestibular cues during self-motion perception. *J. Neurosci.* **29**, 15601–15612 (2009).
159. Mittelstaedt, H. The role of the otoliths in perception of the vertical and in path integration. *Ann. N. Y. Acad. Sci.* **871**, 334–344 (1999).
160. Zu Eulenburg, P., Caspers, S., Roski, C. & Eickhoff, S. B. Meta-analytical definition and functional connectivity of the human vestibular cortex. *NeuroImage* **60**, 162–169 (2012).
161. Guldin, W. O. & Grüsser, O.-J. Is there a vestibular cortex? *Trends Neurosci.* **21**, 254–259 (1998).
162. Lopez, C. & Blanke, O. The thalamocortical vestibular system in animals and humans. *Brain Res. Rev.* **67**, 119–146 (2011).
163. Gurvich, C., Maller, J. J., Lithgow, B., Haghgooie, S. & Kulkarni, J. Vestibular insights into cognition and psychiatry. *Brain Res.* **1537**, 244–259 (2013).
164. Besnard, S., Lopez, C., Brandt, T., Denise, P. & Smith, P. F. Editorial: the vestibular system in cognitive and memory processes in mammalians. *Front. Integr. Neurosci.* **9**, 55 (2015).
165. Smith, P. F. The vestibular system and cognition. *Curr. Opin. Neurol.* **30**, 84–89 (2017).
This paper summarizes the contribution of the vestibular system to high-level cognition, extending beyond reflexes, posture and gaze orientation.
166. Ferrè, E. R. & Haggard, P. Vestibular cognition: state-of-the-art and future directions. *Cogn. Neuropsychol.* **37**, 413–420 (2020).
167. Hitier, M., Besnard, S. & Smith, P. F. Vestibular pathways involved in cognition. *Front. Integr. Neurosci.* **8**, 59 (2014).
168. Guerraz, M., Thilo, K. V., Bronstein, A. M. & Gresty, M. A. Influence of action and expectation on visual control of posture. *Cogn. Brain Res.* **11**, 259–266 (2001).
169. Kim, J. Head movements suggest canal and otolith projections are activated during galvanic vestibular stimulation. *Neuroscience* **253**, 416–425 (2013).
170. Goldberg, J. M., Smith, C. E. & Fernández, C. Relation between discharge regularity and responses to externally applied galvanic currents in vestibular nerve afferents of the squirrel monkey. *J. Neurophysiol.* **51**, 1236–1256 (1984).
171. Fitzpatrick, R. C. & Day, B. L. Probing the human vestibular system with galvanic stimulation. *J. Appl. Physiol.* **96**, 2301–2316 (2004).
172. Gallagher, M., Romano, F., Bockisch, C. J., Ferrè, E. R. & Bertolini, G. Quantifying virtual self-motion sensations induced by galvanic vestibular stimulation. *J. Vestib. Res. Equilib. Orientat.* **33**, 21–30 (2023).
173. Guerraz, M. & Day, B. L. Expectation and the vestibular control of balance. *J. Cogn. Neurosci.* **17**, 463–469 (2005).
174. Yardley, L. Interference between postural control and mental task performance in patients with vestibular disorder and healthy controls. *J. Neurol. Neurosurg. Psychiatry* **71**, 48–52 (2001).
175. Pellecchia, G. L. Postural sway increases with attentional demands of concurrent cognitive task. *Gait Posture* **18**, 29–34 (2003).
176. Vuillerme, N., Nougier, V. & Teasdale, N. Effects of a reaction time task on postural control in humans. *Neurosci. Lett.* **291**, 77–80 (2000).
177. Hunter, M. C. & Hoffman, M. A. Postural control: visual and cognitive manipulations. *Gait Posture* **13**, 41–48 (2001).
178. Lim, J. & Johnson, M. B. Potential mechanisms of retronasal odor referral to the mouth. *Chem. Senses* **36**, 283–289 (2011).
179. Stevenson, R. J., Mahmut, M. K. & Oaten, M. J. The role of attention in the localization of odors to the mouth. *Atten. Percept. Psychophys.* **73**, 247–258 (2011).
180. Spence, C. The tongue map and the spatial modulation of taste perception. *Curr. Res. Food Sci.* **5**, 598–610 (2022).
181. Chaudhari, N. & Roper, S. D. The cell biology of taste. *J. Cell Biol.* **190**, 285–296 (2010).
182. Sclafani, A. Post-ingestive positive controls of ingestive behavior. *Appetite* **36**, 79–83 (2001).
183. Stein, L. J., Nagai, H., Nakagawa, M. & Beauchamp, G. K. Effects of repeated exposure and health-related information on hedonic evaluation and acceptance of a bitter beverage. *Appetite* **40**, 119–129 (2003).
184. Garcia-Burgos, D. & Zamora, M. C. Exploring the hedonic and incentive properties in preferences for bitter foods via self-reports, facial expressions and instrumental behaviours. *Food Qual. Prefer.* **39**, 73–81 (2015).
185. Khorisantono, P. A. et al. Dissociable effects of hunger, exposure and sensory overlap on flavour liking. *Food Qual. Prefer.* **119**, 105211 (2024).
186. Spence, C. Just how much of what we taste derives from the sense of smell? *Flavour* **4**, 30 (2015).
187. Dalton, P., Doolittle, N., Nagata, H. & Breslin, P. A. The merging of the senses: integration of subthreshold taste and smell. *Nat. Neurosci.* **3**, 431–432 (2000).
188. Djordjevic, J. Effects of perceived and imagined odors on taste detection. *Chem. Senses* **29**, 199–208 (2004).
189. Schifferstein, H. N. J. & Verlegh, P. W. J. The role of congruency and pleasantness in odor-induced taste enhancement. *Acta Psychol.* **94**, 87–105 (1996).
This paper reports a classic study that illustrates influences of learned associations on odour-induced taste enhancement.
190. Stevenson, R. J. Confusing tastes and smells: how odours can influence the perception of sweet and sour tastes. *Chem. Senses* **24**, 627–635 (1999).
191. Grabenhorst, F., Rolls, E. T. & Bilderbeck, A. How cognition modulates affective responses to taste and flavor: top-down influences on the orbitofrontal and pregenual cingulate cortices. *Cereb. Cortex* **18**, 1549–1559 (2008).
192. Grabenhorst, F. & Rolls, E. T. Selective attention to affective value alters how the brain processes taste stimuli. *Eur. J. Neurosci.* **27**, 723–729 (2008).
193. Liem, D. G., Miremadi, F., Zandstra, E. H. & Keast, R. S. Health labelling can influence taste perception and use of table salt for reduced-sodium products. *Public Health Nutr.* **15**, 2340–2347 (2012).
194. Chikazoe, J., Lee, D. H., Kriegeskorte, N. & Anderson, A. K. Distinct representations of basic taste qualities in human gustatory cortex. *Nat. Commun.* **10**, 1048 (2019).
195. Crouzet, S. M., Busch, N. A. & Ohla, K. Taste quality decoding parallels taste sensations. *Curr. Biol.* **25**, 890–896 (2015).
196. Porcu, E. et al. Macroscopic information-based taste representations in insular cortex are shaped by stimulus concentration. *Proc. Natl Acad. Sci. USA* **117**, 7409–7417 (2020).
197. Nolden, A. A. & Hayes, J. E. Perceptual and affective responses to sampled capsaicin differ by reported intake. *Food Qual. Prefer.* **55**, 26–34 (2017).
198. Hunter, S. R., Beatty, C. & Dalton, P. H. More spice, less salt: how capsaicin affects liking for and perceived saltiness of foods in people with smell loss. *Appetite* **190**, 107032 (2023).
199. Cowart, B. J. Oral chemical irritation: does it reduce perceived taste intensity? *Chem. Senses* **12**, 467–479 (1987).
200. Lawless, H. & Stevens, D. Effects of oral chemical irritation on taste. *Physiol. Behav.* **32**, 995–998 (1984).
201. Prescott, J., Allen, S. & Stephens, L. Interactions between oral chemical irritation, taste and temperature. *Chem. Senses* **18**, 389–404 (1993).
202. Hamazaki, T., Kaneda, M., Zhang, J., Kaneko, S. & Kajimoto, H. In: *2022 IEEE Haptics Symposium (HAPTICS)* 1–6 (IEEE, Santa Barbara, CA, USA, 2022).
203. Petit, C. E. F., Hollowood, T. A., Wulfert, F. & Hort, J. Colour–coolant–aroma interactions and the impact of congruency and exposure on flavour perception. *Food Qual. Prefer.* **18**, 880–889 (2007).
204. Tu, Y., Yang, Z. & Ma, C. The taste of plate: how the spiciness of food is affected by the color of the plate used to serve it. *J. Sens. Stud.* **31**, 50–60 (2016).
205. Pellegrino, R. & Luckett, C. R. The effect of odor and color on chemical cooling. *Food Qual. Prefer.* **75**, 118–123 (2019).
206. Casillas, M., Rafiee, A. & Majid, A. Iranian herbalists, but not cooks, are better at naming odors than laypeople. *Cogn. Sci.* **43**, e12763 (2019).
207. Olofsson, J. K. et al. A designated odor–language integration system in the human brain. *J. Neurosci.* **34**, 14864–14873 (2014).
208. Lee, B. K. et al. A principal odor map unifies diverse tasks in olfactory perception. *Science* **381**, 999–1006 (2023).

209. Howard, J. D., Plailly, J., Grueschow, M., Haynes, J.-D. & Gottfried, J. A. Odor quality coding and categorization in human posterior piriform cortex. *Nat. Neurosci.* **12**, 932–938 (2009).
210. Sagar, V., Shanahan, L. K., Zelano, C. M., Gottfried, J. A. & Kahnt, T. High-precision mapping reveals the structure of odor coding in the human brain. *Nat. Neurosci.* **26**, 1595–1602 (2023).
211. Gottfried, J. A., Winston, J. S. & Dolan, R. J. Dissociable codes of odor quality and odorant structure in human piriform cortex. *Neuron* **49**, 467–479 (2006).
212. De Araujo, I. E., Rolls, E. T., Velazco, M. I., Margot, C. & Cayeux, I. Cognitive modulation of olfactory processing. *Neuron* **46**, 671–679 (2005).
213. Djordjevic, J. et al. A rose by any other name: would it smell as sweet? *J. Neurophysiol.* **99**, 386–393 (2008).
214. Herz, R. S. & von Clef, J. The influence of verbal labeling on the perception of odors: evidence for olfactory illusions? *Perception* **30**, 381–391 (2001).
This paper reports a classic study illustrating cognitive influences on odour identity perception.
215. Herz, R. S. The effect of verbal context on olfactory perception. *J. Exp. Psychol. Gen.* **132**, 595–606 (2003).
216. Dematte, M. L., Sanabria, D. & Spence, C. Olfactory discrimination: when vision matters? *Chem. Senses* **34**, 103–109 (2008).
217. Morrot, G., Brochet, F. & Dubourdieu, D. The color of odors. *Brain Lang.* **79**, 309–320 (2001).
218. Seo, H.-S. & Hummel, T. Auditory–olfactory integration: congruent or pleasant sounds amplify odor pleasantness. *Chem. Senses* **36**, 301–309 (2011).
219. Shanahan, L. K., Bhutani, S. & Kahnt, T. Olfactory perceptual decision-making is biased by motivational state. *PLoS Biol.* **19**, e3001374 (2021).
220. Zelano, C., Mohanty, A. & Gottfried, J. A. Olfactory predictive codes and stimulus templates in piriform cortex. *Neuron* **72**, 178–187 (2011).
221. Zhou, G. et al. Human olfactory-auditory integration requires phase synchrony between sensory cortices. *Nat. Commun.* **10**, 1168 (2019).
222. Hiratani, N. & Latham, P. E. Rapid Bayesian learning in the mammalian olfactory system. *Nat. Commun.* **11**, 3845 (2020).
223. Pierzchajlo, S. & Olofsson, J. K. In: *Sensory Individuals* (eds Mroczko-Wąsowicz, A. & Grush, R.) 209–224 (Oxford University Press, 2023).
This is a review of cognitive influences on olfaction.
224. Lundström, J. N., Regenbogen, C., Ohla, K. & Seubert, J. Prefrontal control over occipital responses to crossmodal overlap varies across the congruency spectrum. *Cereb. Cortex* **29**, 3023–3033 (2019).
225. Porada, D. K., Regenbogen, C., Seubert, J., Freiherr, J. & Lundström, J. N. Multisensory enhancement of odor object processing in primary olfactory cortex. *Neuroscience* **418**, 254–265 (2019).
226. Pashkovski, S. L. et al. Structure and flexibility in cortical representations of odour space. *Nature* **583**, 253–258 (2020).
227. Wilson, D. A., Fleming, G., Vervoordt, S. M. & Coureaud, G. Cortical processing of configurally perceived odor mixtures. *Brain Res.* **1729**, 146617 (2020).
228. Frederick, D. E. et al. Gamma and beta oscillations define a sequence of neurocognitive modes present in odor processing. *J. Neurosci.* **36**, 7750–7767 (2016).
229. Iravani, B. et al. Odor identity can be extracted from the reciprocal connectivity between olfactory bulb and piriform cortex in humans. *NeuroImage* **237**, 118130 (2021).
230. Stevenson, R. J. Flavor binding: its nature and cause. *Psychol. Bull.* **140**, 487–510 (2014).
This review addresses the phenomenon of perceptual binding between the chemical senses and discusses cortical regulation of the emerging shared percept.
231. Shankar, M. et al. An expectations-based approach to explaining the cross-modal influence of color on orthonasal olfactory identification: the influence of the degree of discrepancy. *Atten. Percept. Psychophys.* **72**, 1981–1993 (2010).
232. Wilson, C. D., Serrano, G. O., Koulakov, A. A. & Rinberg, D. A primacy code for odor identity. *Nat. Commun.* **8**, 1477 (2017).
233. Wilson, D. A. & Stevenson, R. J. The fundamental role of memory in olfactory perception. *Trends Neurosci.* **26**, 243–247 (2003).
234. de Lange, F. P., Heilbron, M. & Kok, P. How do expectations shape perception? *Trends Cogn. Sci.* **22**, 764–779 (2018).
This paper discusses how prior expectations modulate perception and sensory processing in the light of Bayesian models of perception.
235. Badde, S., Myers, C. F., Yuval-Greenberg, S. & Carrasco, M. Oculomotor freezing reflects tactile temporal expectation and aids tactile perception. *Nat. Commun.* **11**, 3341 (2020).
236. Van Ede, F., Jensen, O. & Maris, E. Tactile expectation modulates pre-stimulus β-band oscillations in human sensorimotor cortex. *NeuroImage* **51**, 867–876 (2010).
237. Walsh, K. S., McGovern, D. P., Clark, A. & O'Connell, R. G. Evaluating the neurophysiological evidence for predictive processing as a model of perception. *Ann. N. Y. Acad. Sci.* **1464**, 242–268 (2020).
238. Angelaki, D. E. & Cullen, K. E. Vestibular system: the many facets of a multimodal sense. *Annu. Rev. Neurosci.* **31**, 125–150 (2008).
239. Spence, C. & Bayne, T. In: *Perception and Its Modalities* (eds Stokes, D., Matthen, M. & Biggs, S.) (Oxford University Press, 2014).
240. Yeshurun, Y. & Sobel, N. An odor is not worth a thousand words: from multidimensional odors to unidimensional odor objects. *Annu. Rev. Psychol.* **61**, 219–241 (2010).
241. Green, D. M. & Swets, J. A. *Signal Detection Theory and Psychophysics* (Wiley, 1966).
242. Badde, S. et al. Sensory experience during early sensitive periods shapes cross-modal temporal biases. *eLife* **9**, e61238 (2020).
243. Gallagher, R. M., Suddendorf, T. & Arnold, D. H. Confidence as a diagnostic tool for perceptual aftereffects. *Sci. Rep.* **9**, 7124 (2019).

Acknowledgements

This work was supported by a PRIMA grant (PR00P1_185918/1) from the Swiss National Science Foundation to P.V. J.S. has received funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement n° 947886).

Author contributions

The authors contributed equally to all aspects of the article.

Competing interests

The authors declare no competing interests.

Additional information

Peer review information *Nature Reviews Psychology* thanks Alexis Perez Bellido, Charles Spence and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.