Trends in
Cognitive Sciences

CellPress

Opinion

Orbitofrontal-sensory cortical interactions in learning and adaptive decision-making

Rohan Rao[1,2,3], Hugo Six[4], Aurelio Cortese[4,5,6,*], and Abhishek Banerjee[2,3,*]

The orbitofrontal cortex (OFC) is a hub for value-guided decision-making, linked reciprocally with both cortical and subcortical regions. While projections from sensory areas to the OFC – and vice versa – are known to support goal-directed learning, these projections have often been studied in isolation, and their joint effect remains poorly understood. Here, we revisit these circuits through a unifying computational framework. We propose that sensory cortices send compressed task knowledge to the OFC to build abstract task models, while OFC feedback provides teaching signals that reshape sensory representations within the cortical hierarchy. This bidirectional exchange equips sensory areas with cognitive functions that extend well beyond passive feature detection, with significant implications for our understanding of learning, cognitive models, and artificial neural networks.

Highlights

Reciprocal connections between sensory cortices and the orbitofrontal cortex (OFC) support value computations and the construction of task states during reinforcement-guided learning.

We assess primary sensory cortical projections of task-relevant information to the OFC, including perceptual uncertainty, salience and sensory working memory, departing from classical theories of sensory processing.

OFC feedback projections to sensory areas instruct and enhance sensory representations of task-relevant stimuli.

We propose a synergistic model of closed-loop OFC–sensory cortical interactions that supports efficient learning in the human brain.

The orbitofrontal and sensory cortical circuit in learning

When trying a new café during a morning commute, a rich, flavourful coffee will encourage you to return the next day, whereas a bland one will ensure that you will not. This everyday example illustrates the essence of **reinforcement-guided learning (RL)** (see Glossary), an effective framework for modelling learning processes [1,2]. Among the brain's critical contributors to RL is the orbitofrontal cortex (OFC) [3–5], long recognised for its role in **value computations** and **task-state representation** [6–8]. Damage to the OFC impairs critical components of RL, including credit assignment and response–outcome mappings [9,10]. These computations depend on the OFC's coordinated interaction with several cortical and subcortical brain areas, notably the hippocampus and striatum [11,12]. However, only recently have we begun to unearth the importance of sensory areas' interactions with OFC.

Sensory cortices filter, represent, and relay sensory information, operating within a hierarchically organised system often known as the **sensory hierarchy**. These cortices maintain reciprocal connections with the OFC, supporting the bidirectional exchange of information [13]. Notably, the OFC is among the few frontal regions receiving direct anatomical input from all five sensory modalities [14], enabling multisensory information integration, thought to be necessary to form generalisable value representations [13]. Intriguingly, recent studies have challenged the traditional view of sensory cortices as mere feature detectors, revealing they may accommodate specific cognitive functions such as attention [15], working memory [16], tracking **perceptual uncertainty** [17], and active feature selection [18]. Human neuroimaging studies have even reported value-related coding in sensory areas that may depend on OFC input during RL tasks [19,20].

Despite these findings, research has progressed mainly along parallel tracks – either examining how sensory processing supports OFC function or how OFC modulates sensory functioning –

[1]Biosciences Institute, Newcastle University, Newcastle, UK
[2]Blizard Institute, Queen Mary University of London, London, UK
[3]Adaptive Decisions Laboratory, Department of Pharmacology, University of Oxford, Oxford, UK
[4]Department of Decoded Neurofeedback, ATR Computational Neuroscience Laboratories, Kyoto, Japan
[5]Department of Biomedical Engineering, Sungkyunkwan University, Suwon, South Korea
[6]Center for Neuroscience Imaging Research, Institute for Basic Science, Suwon, South Korea

*Correspondence:
cortese.aurelio@gmail.com (A. Cortese) and
abhishek.banerjee@pharm.ox.ac.uk
(A. Banerjee).

largely overlooking their interaction. This paper aims to re-synthesise our current understanding of **OFC–sensory cortical interactions** during RL in light of new evidence for cognitive computations harboured within sensory cortices. We begin by outlining the anatomical connections between OFC and sensory cortices, then evaluate the roles of 'sensory to OFC' and 'OFC to sensory' pathways. Finally, we propose a conceptual framework in which reciprocal interactions jointly enable efficient RL.

Anatomy of OFC's connectivity with sensory cortices

The anatomical organisation of the OFC and its subregions' contributions to reward-guided decision-making have been extensively reviewed [6,21,22]. OFC occupies areas 10,11,12,13,14 [23,24] and comprises highly interconnected subregions [25]. Barring area 13a, which is agranular, primate OFC is primarily granular, with granularity increasing along a posterior-to-anterior gradient [26]. Given the broad functional and cytoarchitectural similarities between non-human primates (NHPs) and human OFC, findings from NHP studies are often viewed as applicable to human OFC [27], and we draw on them as evidence for human OFC functions. However, cross-species comparisons are not straightforward: while value signals during RL are found in human ventromedial prefrontal cortex/medial OFC (vmPFC/mOFC), they are located in central OFC in monkeys, despite cytoarchitectural and connectivity differences between these regions [28]. Thus, the precise homology between human and primate OFC remains a topic of active debate [28]. As the rodent OFC is agranular, some have argued that it is homologous to the agranular region of the human OFC (area 13a) [27]. In both species, this region shares reciprocal connections with sensory cortices across all modalities and encodes reward value [29], with lesions impairing extinction learning [30]. However, rodents lack a clear homologue of the human granular OFC, and the translational relevance of rodent PFC studies to humans is debated (see [31,32] for detailed reviews). This debate is more contentious than for NHP–human comparisons, likely due to greater phylogenetic distance. Nevertheless, animal models are essential for advancing our understanding of PFC function, as stressed by many [31,32]. Throughout this paper, we indicate when findings from rodent OFC studies are used to support our claims.

In humans and NHPs, the OFC maintains reciprocal connections with a mixture of primary and higher sensory cortices across modalities [13,33] (Figure 1A). These inputs are more prominent in the lateral OFC (lOFC) than the mOFC [25]. The OFC is considered a higher-order olfactory and gustatory cortex, receiving strong inputs from the respective primary sensory areas. It also connects with primary and higher somatosensory cortices, while visual and auditory inputs arise predominantly from association areas, such as the ventral visual stream and belt/parabelt auditory regions [34,35]. These projections to the OFC spanning heterogeneous levels of sensory hierarchy have been hypothesised to convey stimulus identity signals [33], such as object and face recognition from the inferior temporal, fusiform, and rhinal cortices [34]. We discuss the evidence for this hypothesis and other functions of feedforward sensory to OFC projections in the next sections.

Interestingly, posterior OFC receives more inputs from primary sensory areas, while anterior OFC receives more from association areas [14]. Though some studies report structural and functional OFC connectivity with primary visual and auditory cortices in humans [20,33,36–38], these are not consistently supported by tracer studies and are therefore not the focus here. Notably, based on corticocortical interconnectivity findings, the OFC overlaps with broader 'orbital' and 'medial' prefrontal networks [25] implicated in sensory integration and emotional regulation hubs, respectively [39].

Sensory projections to OFC

What is the functional role of bottom-up sensory inputs to OFC? This question has received considerable attention across species in recent decades [40–42]. Here, we first review the

Glossary

Bottom-up attentional capture: allocation of attention to a stimulus that is sufficiently salient, driven by the sensory properties of the stimulus that might differ from top-down attended features.

Cognitive map: the systematic organisation of physical or abstract entities and the relationship between them in artificial or biological neural systems.

OFC–sensory cortical interactions: the anatomical and functional direct and indirect connections between the orbitofrontal cortex and sensory cortices from all five sensory modalities.

Perceptual uncertainty: the degree of ambiguity in the agent's perception of stimuli in its environment, which can arise from various sources, including sensory noise, ambiguity in the environment, and uncertainty in the agent's internal models.

Reinforcement-guided learning (RL): a trial-and-error learning process shaped by rewarding and aversive outcomes.

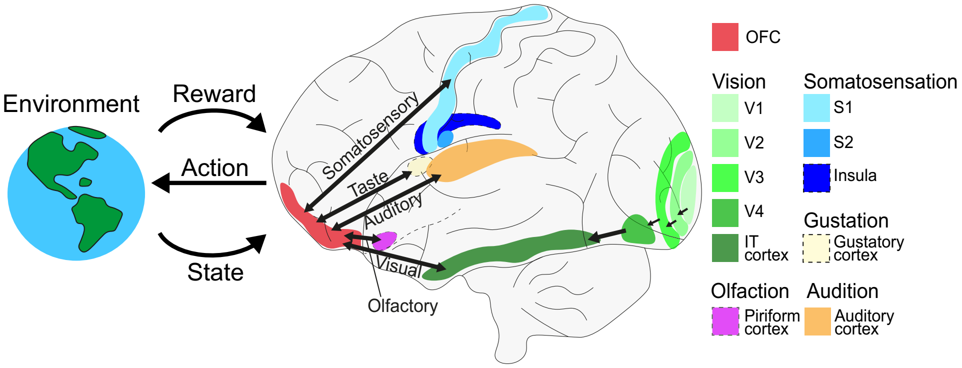
Representation learning: learning a representation of the environment based on sampled stimuli that makes it easier to extract useful information according to the agent's goal.

Sensory hierarchy: classical hierarchical organisation of sensory processing in the brain, where primary sensory areas receive thalamic projections of sensory information and encode sensory feature information before relaying this information to higher-order sensory areas involved in higher functions such as object recognition.

Sensory working memory: the storage and recall of sensory information by an artificial or biological neural system for a short duration after the relevant information is no longer observable.

Task-state representation: collection of observable and non-observable information necessary to predict decision outcomes. The transitions between task states constitute a Markov decision process that allows RL algorithms to solve the reward maximisation problem.

Value computations: the process by which the brain represents, updates and manipulates subjective values associated with stimuli or actions using sensory information, prior knowledge and goals.



Trends in Cognitive Sciences

Figure 1. Major anatomical connections between sensory cortices and the orbitofrontal cortex (OFC). A lateral view of the major anatomical connections between orbitofrontal and sensory cortices in the human brain. The OFC shares reciprocal anatomical connections with sensory and association cortices from all sensory modalities [14]. These cortices include (i) primary and secondary somatosensory cortex (S1 and S2), somatosensory insula and the frontal operculum [14]; (ii) primary gustatory cortex for gustation [14]; (iii) piriform cortex, entorhinal cortex and anterior insula for olfaction [14,35]; (iv) the superior temporal gyrus, including the auditory rostral belt and parabelt for audition [35]; (v) the inferior temporal cortex (IT), perirhinal cortex and the superior temporal sulcus for vision [34]. As granularity increases from the OFC's posterior-to-anterior gradient, multimodal sensory inputs also become sparser [26]. These anatomical connections enable the OFC (in particular, posterior OFC) to integrate multimodal sensory information from the environment about current states and rewards to support action selection during reinforcement learning tasks. Anatomical connectivity in this context is based on tracer studies in non-human primates. Dotted outlines indicate interior brain areas. Abbreviations: V1, primary visual cortex; V2–V4, higher visual cortices.

Value remapping: update of the value or reward associated with a stimulus or action based on new information or experience, enabling the adaptation of behaviour to a changing environment.

prevailing view in systems neuroscience that these inputs merely provide the OFC with sensory information during RL. We then update this perspective in light of recently discovered cognitive functions of sensory cortices and emerging theories on the OFC's role in representing latent task states.

How do sensory inputs classically support OFC value computations?

RL unfolds as a series of interactions between an agent and its environment, typically through trial-and-error (Figure 1A). First, the agent estimates the current state from environmental inputs and its latent knowledge (value expectation, or an internal model of the world). It then selects an action that maximises future returns. The agent finally updates its latent knowledge based on the outcome (rewarding, aversive or neutral). From a computational perspective, the human OFC appears to be a critical component in many RL algorithms (Box 1), involved in distributed value computations and state representations (Figure 2A). These value computations include encoding subjective value [7], reward prediction errors (RPEs, in lOFC) [19], value comparisons (mOFC) [9,43], reward identity (lOFC) [41], and credit assignment (lOFC) [9,20]. Although these computations serve distinct roles within RL, many of them depend on inputs from sensory cortices to the OFC.

Sensory cortices are thought to provide the OFC with essential information about environmental features, task uncertainty, and volatility inferred from stimuli statistics – enabling context-sensitive value encoding [42]. For instance, when we enjoy a cup of coffee, OFC neurons are thought to compute its subjective value by integrating sensory inputs (e.g., flavour, colour, and texture) with cognitive signals from subcortical regions. These include emotional inputs from the amygdala (e.g., stress [44]), physiological states from the hypothalamus (e.g., hunger [45]), and reward or RPE information from the nucleus accumbens, ventral striatum and dopaminergic ventral tegmental area (VTA) pathways [12,46,47]. Additionally, contextual and memory-related information from the subcortical hippocampus and prefrontal cortical areas (e.g., brand reputation [11,48,49])

Box 1. RL and the OFC

RL provides a powerful framework to study decision-making. Yet, its neural implementation remains debated [53]. Here, we introduce several RL formalisms that could be supported by OFC–sensory interactions (Figure I).

Model-free RL involves learning a decision policy through trial-and-error without explicitly modelling environmental dynamics, aiming to maximise cumulative reward [2]. While the OFC may play a limited role in model-free learning [120], it contributes useful representations of reward values [7] and exploratory behaviour [3].

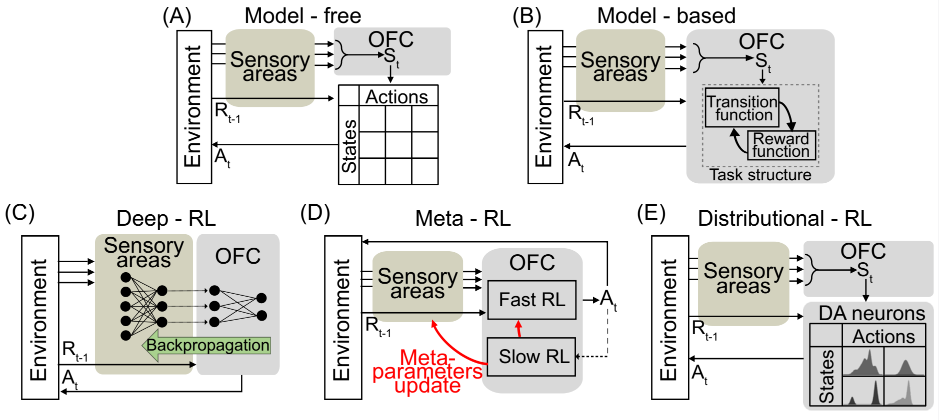
Model-based RL builds a model of the environment (i.e., state transitions) to guide decision-making [2]. The OFC supports this by encoding both current task states and higher-level abstracted task structure [88], binding sensory and latent information to form cognitive maps of task space [89].

Deep-RL leverages deep neural networks to handle high-dimensional state spaces [121]. Though originally applied to vision [122], recent work extends deep RL to model higher cognitive functions [123], including value encoding in the OFC via recurrent neural networks [124]. This architecture offers a compelling framework for modelling OFC–sensory interactions. For instance, bottom-up feature extraction through feedforward computation and top-down learning signals through backpropagation or other novel credit-assignment mechanisms such as prospective configuration [125].

Meta-RL allows agents to learn across tasks and timescales by updating meta-parameters through parallel reinforcement procedures [114,126]. These models learn ‘how to learn’ and generalise across contexts. Recurrent networks trained via meta-RL replicate key aspects of OFC dynamics during reversal learning in mice [115]. However, improved value discriminability shown by the model was not observed experimentally – possibly because learning computations shifted to sensory areas via OFC feedback.

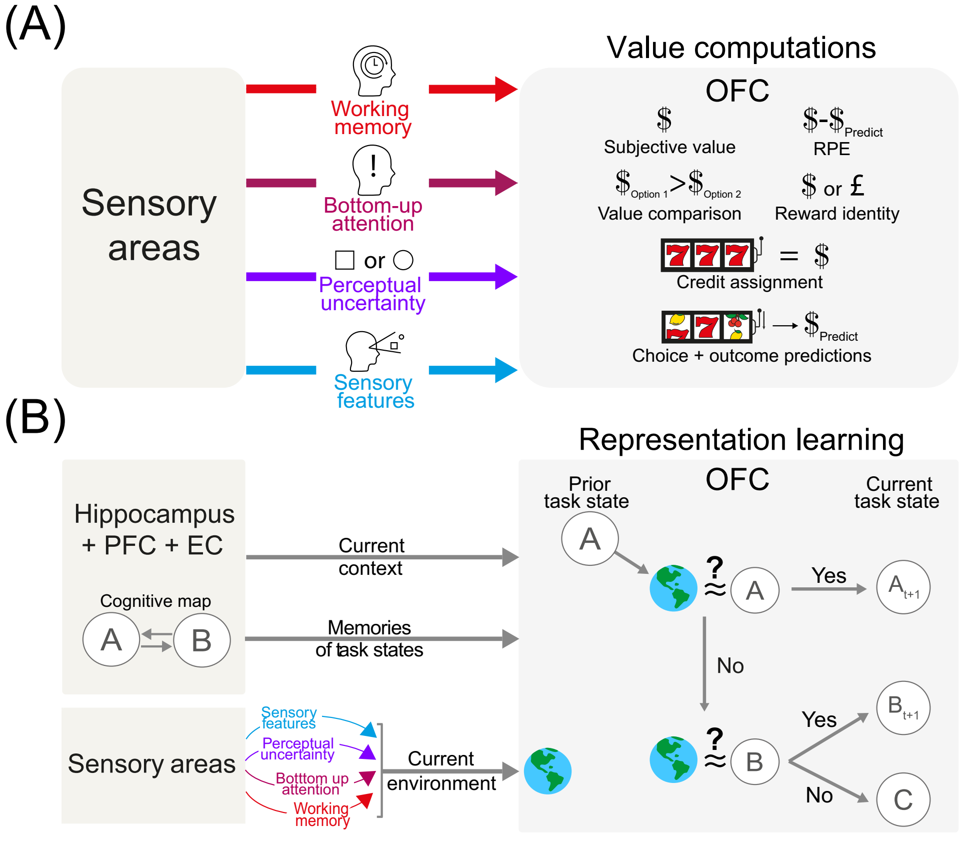
Distributional RL extends standard RL by learning full reward distributions for state-action pairs rather than single expected values [127]. This captures variability in outcomes and supports more flexible decision-making. While direct evidence in OFC is limited, recent findings show OFC neurons may be tuned to stimuli near the tails of reward distributions [128].

Separately from RL, OFC may play roles in other cognitive frameworks, such as signalling ‘belief states’ within Bayesian inference frameworks [129]. Many of these models are not mutually exclusive, and studies have suggested they may even be used in parallel in certain tasks [53]. Thus, a possible reconciliation of these frameworks in the brain is that they are task and context-specific, with OFC, vlPFC, and frontopolar cortices potentially coordinating model arbitration [53].



Trends in Cognitive Sciences

Figure I. Role of the orbitofrontal cortex (OFC) in reinforcement-guided learning (RL). (A) In model-free RL, the OFC may simply encode cached task state-action values. (B) In model-based RL, OFC may build the task space as a set of transition and reward functions (thus further tracking hidden task states, reward value, reward identity and stimulus-reward association). (C) In deep-RL, the OFC may represent deeper layers encoding high-level value and/or policy layers. The top-down teaching signal from the OFC to sensory areas may be a sophisticated backpropagation process. (D) In Meta-RL, the OFC may track variables related to both the activity-based (Fast RL) as well as the plasticity-based (Slow RL). Plasticity-based RL process may control meta-parameters encoded directly in sensory areas. (E) In distributional RL, potentially similar to the model-free RL, the OFC may encode entire distributions of task states with cached values. Abbreviations: A_t, current trial’s chosen action; R_{t-1}, previous trial reward; S_t, current trial’s state. Reward distributions used in (E) are adapted from recent work [127].



Trends in Cognitive Sciences

Figure 2. Contribution of sensory inputs to value computation and representation learning in the orbitofrontal cortex (OFC). (A) Schematic illustrating how the OFC may use higher-order cognitive information from sensory cortices to perform value computations. The OFC may use perceptual uncertainty signals [70] to modulate the strength of reward identity, credit assignment and outcome prediction codes [72,74]. Bottom-up attention and salience signals [15] highlight relevant stimuli and choices during reward learning [57], such as a slot machine catching your eye in a casino. Sensory working memory [67] can be used to compare sensory features of perceptually similar stimuli that predict reward, facilitating value comparison and credit assignment. (B) Proposed mechanism for representation learning in the OFC. Sensory inputs filtered through cognitive computations are integrated with contextual and memory information to compare perceived environments to a prior state 'A' [76]. If dissimilar, the OFC checks for similarity with previously experienced states (e.g., state 'B'), which are stored in the hippocampus, entorhinal cortex (EC), and other prefrontal cortex (PFC) regions [11,76,82,83]. If no match is found, the OFC defines a novel state 'C' [76] with an associated exploration bonus [3] for new options, supporting adaptive learning. Abbreviation: RPE, reward prediction error.

reaches the OFC. Intriguingly, rodent studies have shown that OFC population-level value responses may emerge from subpopulations of 'pessimistic' and 'optimistic' neurons that underestimate and overestimate, respectively, the utility and probability of reward [50], a mechanism that could extend to primates.

The importance of sensory inputs to OFC in value-based decisions has been illustrated through chemogenetics silencing of perirhinal cortex projections to the OFC, which reduced sensitivity to reward magnitude and disrupted expected value computations [42]. As the perirhinal cortex is often considered an extension of the 'ventral visual stream' and is associated with object recognition, these findings suggest that the OFC integrates stimuli, or event, identity information with reward associations to inform choices.

The OFC transmits integrated value signals via local circuits that compute comparisons between options, and disrupting these signals (electrically or pharmacologically) impairs behaviour [4,43]. Its access to multimodal sensory inputs presumably allows integration of rewards across modalities – for example, combining gustatory and olfactory features of coffee into a unified scalar value [51]. Supporting this view, subpopulations of OFC neurons encode sensory-specific value [52], which may be combined to enable cross-modal value comparisons. Although value signals also exist in the dopaminergic system [47], the OFC stands out for its consistent value representations across tasks [53].

To support optimal decisions in RL, the lOFC assigns value to specific stimuli and actions – a process known as credit assignment [9,42]. This likely relies on dynamic interactions with sensory cortices, which can provide real-time contextual information [42]. When rewards are immediate, lOFC neurons could integrate sensory inputs with reward signals from the ventral striatum and dopaminergic systems [12,47]. For delayed rewards, it may draw on contextual and mnemonic information from the hippocampus, prefrontal cortex, and working memory [11,48,49,54]. Sensory inputs may thus modulate credit assignment strength in both cases, enabling flexible value comparisons across time and contexts.

Sensory areas precompute task information to support OFC value computations

In value computations, projecting sensory information about observable environmental features to the OFC is a core function of sensory cortices. But they may also transmit higher-order cognitive signals, such as stimulus salience – how much a stimulus stands out – encoded via saliency maps [55] and population activity patterns [56]. This **bottom-up attentional capture** can influence prefrontal areas, including the OFC [57,58] (Figure 2A). For instance, OFC neurons have been shown to transiently encode the value of a luminance-changing cue even when it lacked predictive value [57], suggesting salience alone can modulate OFC activity. Since salient stimuli often signal potential rewards or punishments [59], they may accelerate OFC value coding [57,58] (Figure 2A). Consistent with this interpretation, rats' ventral/lateral OFC neurons preferentially encode salient stimuli, regardless of reward association [60]. The OFC may improve credit assignment and facilitate learning in complex environments by amplifying salient inputs. However, it remains unclear whether salience inputs to the OFC come primarily from sensory cortices or other brain areas such as the mediodorsal thalamus and the inferior frontal gyrus [61,62].

Beyond bottom-up attentional capture mechanisms, sensory cortices also support **sensory working memory** [63–65]. Sensory neurons can maintain stimulus representations after offset through sustained activity, population coding, and oscillatory synchrony with the prefrontal cortex [16,64–66]. The fidelity of these representations can even predict behavioural performance during delayed discrimination tasks [67]. This function could be especially useful during credit assignment, where the OFC must discriminate between multiple stimuli or their combinations. While the hippocampus and PFC also provide working memory signals to the OFC [54], sensory cortex inputs may deliver more precise, real-time information about recent stimuli (Figure 2A).

When faced with noisy or ambiguous input, the brain must evaluate competing interpretations of the environment. A useful concept here is perceptual uncertainty, the inverse of how confidently an agent can identify the true signal. Perceptual uncertainty aligns well with the Bayesian perspective, in which probabilistic neural codes in sensory areas simultaneously encode the estimated identity (mean) and uncertainty (variance) of a stimulus [68]. Information about stimulus uncertainty and probability [69,70] could provide valuable information for downstream computations in regions like the OFC. Indeed, higher visual cortices, such as the inferior temporal cortex, have been shown to have enhanced connectivity with frontal cortices in trials with high perceptual uncertainty [70]. It is worth noting that the OFC itself is thought to track perceptual uncertainty as a scalar signal [71]. The OFC might further integrate perceptual uncertainty with other sources of uncertainty (e.g., reward probability [72]) to generate abstract belief or confidence signals, guiding action selection [73]. Confidence signals may also intrinsically modulate value computations in the OFC (Figure 2A). Indeed, one of our laboratories found that higher perceptual uncertainty corresponded to reduced value-related activity in the mOFC/vmPFC [74]. Relayed to the OFC, these sensory signals could refine outcome predictions for perceptually similar stimuli.

How do sensory areas support task representations in the OFC?

While traditionally associated with value computations, a parallel research stream suggests that lOFC [11] and mOFC/vmPFC [75] also represent abstract task states within a non-spatial **cognitive map** (see [6,76]). Proposed by Tolman [77] and later supported by hippocampal studies [78], the cognitive map concept has been expanded to encompass abstract task structures [79,80]. A key study [7] found that mOFC selectively encoded task-relevant observable variables (in the current trial) and latent variables (relevant information in the previous trial) but not task-irrelevant variables, indicating its role in representing the current task state [8]. This abstract representation allows the OFC to guide behaviour via projections to the striatum, ACC, and lateral PFC [79,81], supporting RL, generalisation, and continual learning.

We propose that sensory cortices are central to the OFC's ability to efficiently construct task-state representations – a process known as **representation learning** [76]. The OFC may compare incoming sensory inputs with stored task states in the hippocampus and entorhinal cortex [82,83]. If the input matches a known state, the OFC reuses and updates that memory; if not, it generates a new state. Algorithmically, this could involve sequential comparisons (Figure 2B). For instance, an agent currently in state 'A' might: (i) update their current state to 'A_{t+1}' if the input is similar; (ii) switch to a known state 'B'; or (iii) create a new state 'C'. Sensory cortices may additionally compress and relay features like salience, working memory content, and perceptual uncertainty to support this process. Updated states can then be sent back to memory systems and other prefrontal areas, continuously recalibrating the brain's internal cognitive map [11,82,83].

Our proposal aligns with models of hippocampal function that balance pattern separation and generalisation [84], and echoes recent computational models of working memory that invoke similar mechanisms [85]. We suggest that sensory cortices provide the OFC with precomputed, compressed task knowledge (stimuli identity, uncertainty, past stimuli, salience) that support the construction of task states [20,80,86]. While sensory cortices do not have access to the whole set of associations as the OFC or hippocampus might have, they can still reduce the dimensionality of this sensory input in a useful manner, that is, they can 'compress' task knowledge. This early-stage dimensionality reduction at the sensory level may facilitate representation learning in the OFC. This idea also aligns with recent theories of compositionality, which propose that both biological and artificial systems build complex representations by combining simpler, reusable components [87].

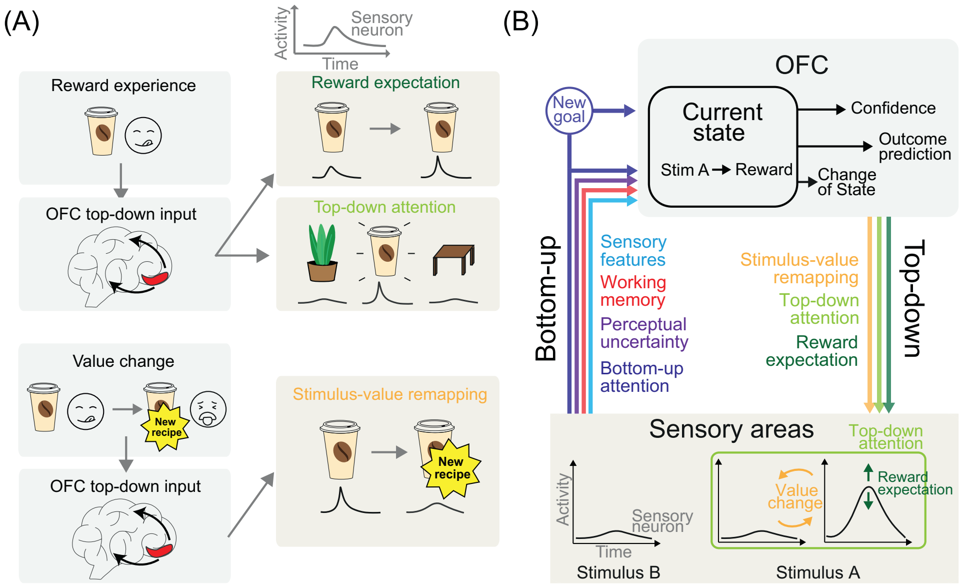
Recent research suggests that the OFC additionally encodes broader cognitive maps – representations of the relationships between task elements or states [88,89]. These maps are well suited for supporting model-based RL (Box 1) as they help predict how actions lead to state transitions. Cognitive maps (or meta-maps) likely span the OFC, the hippocampus, the entorhinal cortex and other prefrontal regions [48,82,83], though how this information is distributed across these regions remains under investigation. Notably, hippocampal-to-OFC theta oscillations may transmit state information, with the OFC preferentially encoding state-dependent values rather than states themselves [90]. Developing theoretical frameworks that reconcile OFC's function in task-state representation and state-dependent valuation will be essential moving forward.

OFC control signals to sensory areas support RL

Similar to bottom-up sensory to OFC projections, the function of top-down projections has been studied across species in the context of RL [19,91]. Intriguingly, these top-down projections may drive reward expectation [92], value-driven attentional capture [93], and coding remapping [19] directly within sensory areas. In the following sections, we review the evidence supporting these functions and discuss their implications for sensory processing during RL.

OFC control signals improve perceptual processing in sensory areas

Value signals can enhance perception [20,94], with high-reward stimuli often more accurately discriminated than low-reward ones [95]. One mechanism may involve OFC-derived teaching signals that adjust gain or receptive fields in sensory cortices based on reward history or expectations [92] (Figure 3A). Rodent studies reveal modality-specific pathways for this effect. In vision,



Trends in Cognitive Sciences

Figure 3. The orbitofrontal cortex (OFC)–sensory cortex interactions supporting reinforcement-based adaptive learning. (A) Following a rewarding experience (e.g., an enjoyable coffee), the OFC can engage two complementary top-down mechanisms. First, it sends a reward-expectation signal that enhances the encoding strength of sensory neurons for stimuli associated with reward [99]. Second, the OFC issues a goal-directed attentional signal [93] that increases sensory neuron responses to goal-relevant stimuli while filtering out irrelevant stimuli. Both mechanisms sharpen neuronal representations of relevant stimuli, resulting in enhanced perception and improved sensory acuity for task-relevant features. Otherwise, when a stimulus' value changes abruptly (e.g., the coffee becomes unpleasant), the OFC can send top-down remapping signals to sensory cortices [19,91]. These signals dampen neural responses to the previously rewarding stimulus, supporting rapid behavioural adaptations. (B) In our proposed model, sensory cortices send multiple information streams to the OFC: sensory features help to construct OFC task states. Bottom-up attention directs the OFC to prioritise salient stimuli, which may trigger updates to task state or goals. Sensory working memory enables discrimination between similar stimuli (e.g., distinguishing task-relevant stimulus A from a recent but irrelevant stimulus B), improving outcome predictions. These predictions in turn drive top-down reward expectation and value-remapping signals back to sensory cortices. Perceptual uncertainty reflects the reliability of stimulus representations and informs OFC confidence estimates that modulate its outputs, enhancing signals under high certainty and decreasing signal strength when confidence is low. OFC remapping signals enable rapid neural re-tuning during changes in task context.

OFC projections to primary visual cortex (V1) somatostatin interneurons suppress responses to unrewarded stimuli [96]; in audition and olfaction, projections to excitatory and inhibitory neurons in primary auditory cortex (A1) and piriform cortex amplify responses to reward-associated stimuli [97,98]. These findings suggest conserved mechanisms by which the OFC can modulate higher visual (e.g., fusiform cortex [99]) and auditory regions (belt areas and superior temporal gyrus [100]) to support perception via value-based feedback. Note that OFC-to-primary visual and auditory cortex (A1, V1) projections appear unique to rodents. Complementary to reward expectation, value-driven attentional capture enhances perception across modalities: stimuli linked to reward or punishment reliably draw attention in both visual and auditory domains [101,102]. This is typically attributed to frontoparietal control networks, which modulate sensory cortices via long-range projections [103]. However, the OFC may also directly influence sensory cortices, strengthening task-relevant sensory representations via its own projections [93]. This mechanism could act synergistically with frontoparietal and midbrain (e.g., VTA) inputs [104] to sharpen task-relevant perception during RL (Figure 3A).

It is important to mention that the OFC connects with higher-order visual and auditory cortices, but with both primary and higher cortices in other sensory modalities. This anatomical pattern suggests that top-down OFC signals may selectively enhance perception at the level of what is typically most relevant for behaviour, such as stimulus identity in vision (e.g., objects [99]) and audition (e.g., speech [100]). While in other modalities, these signals may additionally modulate feature-level discrimination. Since rodents exhibit direct projections from OFC to the primary visual [96] and auditory cortices [97], there may be evolutionary divergence in the role and granularity of OFC top-down control across species.

OFC signals can remap value encoding in sensory areas

OFC projections to sensory cortices can enact **value remapping**, that is, signal abrupt changes in stimulus-outcome contingencies (Figure 3A) [19,91]. In one of our laboratories, we investigated these top-down ‘teaching’ signals using fMRI during a probabilistic tactile reversal learning task [21]. Following contingency reversal, we observed a transient increase in functional connectivity between the lOFC and ipsilateral reward-selective regions of primary somatosensory cortex (S1), which declined as participants adapted. Crucially, lOFC outcome-related activity preceded S1 responses during the reversal phase, consistent with lOFC-driven reconfiguration of sensory-reward representations to support flexible behaviour. Nevertheless, confirming the directionality of these signals will require causal methods such as Granger causality, transcranial stimulation, or neurofeedback-based approaches [105,106]. LOFC activity also decreases with learning expertise, decreasing as participants move from naïve to expert phases [19]. This mirrors findings that PFC engagement decreases as performance becomes more efficient [107], possibly reflecting a reduction in cognitive demands. One interpretation is that, during expert phases, reward-related responses become stable and selective in sensory areas such as S1 [19], the auditory belt [108], primary gustatory cortex [109], and the inferior temporal cortex [110] – allowing these areas to assume greater value processing roles. This shift may offload computational burden from lOFC once stimulus-action mappings are well established [19]. Lesion studies nonetheless offer a nuanced picture: while OFC damage impairs reversal learning and increases lose-stay behaviour in probabilistic tasks [111], it has minimal effects in deterministic settings [112]. This suggests that OFC switch signals may be particularly relevant in uncertain environments in primates.

Complementing correlational findings in humans and primates, rodent studies offer causal evidence for OFC-driven value remapping in sensory cortices. In one study from one of our laboratories, mice performed a tactile Go/No-Go reversal learning task [91]. Following reversal, a fraction of value- and outcome-selective S1 neurons initially lost their selectivity but reacquired it with learning – unless lOFC➔S1 projections were silenced, which abolished both neural remapping and behavioural adaptation. Further analyses revealed that this top-down signal also remapped S1 reward-expectation selectivity and resembled a context-prediction error [113]. Such a signal is consistent with model-based and meta-RL frameworks (Box 1), as it supports generalisation by updating stimulus-outcome expectations even for unobserved stimuli following reversal [114,115].

Closing the loop through a holistic RL framework of OFC and sensory interactions

Most RL research treats bottom-up sensory inputs to OFC and top-down OFC projections to sensory areas as separate processes. Mirroring this approach, we introduced their roles separately. But this division overlooks their dynamic interaction. In reality, bottom-up inputs can shape precise top-down signals, and vice versa. We now propose a closed-loop framework that captures how synergy between these pathways can benefit RL.

In our framework, sensory inputs help build and update accurate task-state representations in the OFC (Figure 3B), encoding all relevant variables, including predictions of prospective outcomes. These internal OFC states then guide precise reward expectations and attentional signals, which, in turn, enhance perception of task-relevant features. Such a reciprocal loop reduces perceptual uncertainty, sharpens neural representations, and supports adaptive behaviour by continuously aligning sensory processing with task demands [56].

Reversal learning is a second key context to discuss the importance of reciprocal OFC-sensory interactions in RL. After reversal, top-down OFC signals may remap outcome and expectation responses in sensory cortices. These areas, in turn, may integrate sensory-reward signals with higher-order cognitive information to deliver compressed, task-relevant inputs back to OFC for task-state reconstruction and comparison. Additionally, sensory inputs conveying perceptual uncertainty may modulate the strength of OFC feedback. In ambiguous contexts, lower decision confidence [73] could weaken or diffuse OFC signals, resulting in less precise modulation of sensory encoding that reflects uncertainty in credit assignment.

While several perspectives on OFC function in RL exist (Box 1), our framework emphasises the OFC's role in constructing task-state representations within a broader 'world model' or cognitive map, concepts often linked to model-based and meta-RL. Our framework, however, does not exclude other algorithmic implementations such as model-free RL, which we suspect may be engaged differentially depending on task demands, behavioural strategies, or environmental context, potentially shaping top-down teaching signals. Although our focus is on OFC-sensory interactions in task-state representation, choice, and learning, we recognise the critical roles of other regions – including the hippocampus, entorhinal cortex, midbrain, and mesolimbic system – in supporting RL [53]. We thus position our proposal as one flexible component within a broader, distributed neural architecture that supports RL.

Concluding remarks

The functional role of sensory cortices in cognition has undergone a profound shift. Once considered passive encoders of physical features – such as tonotopic [116], somatotopic maps [117], or visual receptive fields [118] – they are now recognised as active contributors to higher-order functions. This reappraisal carries important, yet underexplored, implications for how sensory projections influence executive regions, such as the OFC, during learning and decision-making.

We have highlighted how sensory cortices contribute to bottom-up attention [15], sensory working memory [16] and perceptual uncertainty [17], and how these signals, when projected to the

Outstanding questions

Are the mechanisms underpinning OFC teaching signals to sensory areas distinct across task space and task type? Are they conserved across species, and what might that signify?

What function do value representations in sensory areas play in value-guided decision-making?

Is value an abstract state in RL? If so, how can this be integrated into RL models?

How are value and task-state representations in OFC used to create teaching signals that cause plasticity changes in sensory areas?

Do unilateral and bilateral coupling measures between OFC and sensory cortices in human learning studies generalise across sensory modalities?

Is the underlying mechanism of top-down OFC teaching signals to sensory cortices consistent across sensory modalities?

What is the role of intrinsic value signals, for example, derived from affective computations?

What happens when value and sensory-OFC loops converge on the wrong dimension(s)?

Does silencing of salience, perceptual uncertainty, or working memory encoding neurons in sensory cortices alter OFC task representations?

OFC, can support value computations and representation learning. We also discussed how top-down OFC signals may enhance the encoding of task-relevant and reward-associated stimuli in sensory cortices, potentially improving perception and redistributing value computations from the OFC to sensory areas. While some of these ideas are speculative, the role of value coding in sensory cortices during RL is a promising direction for future research (see Outstanding questions). These insights extend beyond neuroscience (Box 1), suggesting that AI systems (which often neglect cognitive roles for sensory units) may benefit from incorporating such dynamics. While some mechanisms – like concept-specific units [119] – can arise in deep learning models, others, such as top-down modulation of sensory representations, are not easily captured by standard backpropagation. Whether OFC-like tuning shifts can be modelled in artificial systems remains an exciting challenge.

In sum, we proposed a framework in which reciprocal OFC-sensory cortex interactions dynamically support RL. Future work should test these bidirectional circuits through carefully designed experiments (see Outstanding questions). Ultimately, we advocate moving beyond simple ‘A-to-B/B-to-A’ models towards an integrative, systems-level understanding (‘A and B’) of the circuitry underlying value-guided behaviour.

Acknowledgments

We thank Edmund T. Rolls and Kazuhisa Shibata for comments on an earlier draft of this manuscript. We also thank Banerjee and Cortese laboratory members for helpful discussions. This work was supported by the Reece Foundation (R.R. and A.B.); Wellcome Trust Institutional Strategic Award (A.B.), a Royal Society research grant (RGS\R2\202155, to A.B.), a Wellcome Trust Career Development Award, and previously a Novo Nordisk Foundation Young Investigator Award (both to A.B.); A. B. is affiliated to the Digital Environment Research Institute at QMUL and the Department of Psychiatry at University of Oxford; JSPS KAKENHI Grant Number JP22H05156 (H.S., A.C.), Innovative Science and Technology Initiative for Security Grant Number JPJ004596, ATLA, Japan (H.S., A.C.).

Declaration of interests

No interests are declared.

Declaration of generative AI and AI-assisted technologies in the writing process

Grammarly and generative AI tools were used for proofreading, grammatical corrections, and targeted suggestions to enhance sentence clarity. After using these tools, all authors reviewed and edited the manuscript, taking full responsibility for its contents.

References

1. Schultz, W. *et al.* (1997) A neural substrate of prediction and reward. *Science* 275, 1593–1599
2. Sutton, R.S. and Barto, A.G. (2018) *Reinforcement Learning: An Introduction*, MIT Press
3. Costa, V.D. and Averbeck, B.B. (2020) Primate orbitofrontal cortex codes information relevant for managing explore-exploit tradeoffs. *J. Neurosci.* 40, 2553–2561
4. Setogawa, T. *et al.* (2019) Neurons in the monkey orbitofrontal cortex mediate reward value computation and decision-making. *Commun. Biol.* 2, 126
5. Banerjee, A. *et al.* (2021) Reinforcement-guided learning in frontal neocortex: emerging computational concepts. *Curr. Opin. Behav. Sci.* 38, 133–140
6. Knudsen, E.B. and Wallis, J.D. (2022) Taking stock of value in the orbitofrontal cortex. *Nat. Rev. Neurosci.* 23, 428–438
7. McGinty, V.B. and Lupkin, S.M. (2023) Behavioral read-out from population value signals in primate orbitofrontal cortex. *Nat. Neurosci.* 26, 2203–2212
8. Schuck, N.W. *et al.* (2016) Human orbitofrontal cortex represents a cognitive map of state space. *Neuron* 91, 1402–1412
9. Noonan, M.P. *et al.* (2017) Contrasting effects of medial and lateral orbitofrontal cortex lesions on credit assignment and decision-making in humans. *J. Neurosci.* 37, 7023–7035
10. Rudebeck, P.H. *et al.* (2017) Specialized representations of value in the orbital and ventrolateral prefrontal cortex: desirability versus availability of outcomes. *Neuron* 95, 1208–1220
11. Mızrak, E. *et al.* (2021) The hippocampus and orbitofrontal cortex jointly represent task structure during memory-guided decision making. *Cell Rep.* 37, 110065
12. Jenni, N.L. *et al.* (2022) Distinct medial orbitofrontal–striatal circuits support dissociable component processes of risk/reward decision-making. *J. Neurosci.* 42, 2743–2755
13. Rolls, E.T. *et al.* (2020) The orbitofrontal cortex: reward, emotion and depression. *Brain Commun.* 2, fcaa196
14. Carmichael, S.T. and Price, J.L. (1995) Sensory and premotor connections of the orbital and medial prefrontal cortex of macaque monkeys. *J. Comp. Neurol.* 363, 642–664
15. Wang, S. *et al.* (2021) Awareness-dependent normalization framework of visual bottom-up attention. *J. Neurosci.* 41, 9593–9607
16. Hallenbeck, G.E. *et al.* (2021) Working memory representations in visual cortex mediate distraction effects. *Nat. Commun.* 12, 4714
17. Van Bergen, R.S. *et al.* (2015) Sensory uncertainty decoded from visual cortex predicts behavior. *Nat. Neurosci.* 18, 1728–1730
18. Downer, J.D. *et al.* (2021) An emergent population code in primary auditory cortex supports selective attention to spectral and temporal sound features. *J. Neurosci.* 41, 7561–7577

19. Wang, B.A. *et al.* (2023) Human orbitofrontal cortex signals decision outcomes to sensory cortex during behavioural adaptations. *Nat. Commun.* 14, 3552
20. Cortese, A. *et al.* (2021) Value signals guide abstraction during learning. *eLife* 10, e68943
21. Rushworth, M.F.S. *et al.* (2011) Frontal cortex and reward-guided learning and decision-making. *Neuron* 70, 1054–1069
22. Klein-Flügge, M.C. *et al.* (2022) Medial and orbital frontal cortex in decision-making and flexible behavior. *Neuron* 110, 2743–2770
23. Öngür, D. *et al.* (2003) Architectonic subdivision of the human orbital and medial prefrontal cortex. *J. Comp. Neurol.* 460, 425–449
24. Carmichael, S.T. and Price, J.L. (1994) Architectonic subdivision of the orbital and medial prefrontal cortex in the macaque monkey. *J. Comp. Neurol.* 346, 366–402
25. Carmichael, S.T. and Price, J.L. (1996) Connectional networks within the orbital and medial prefrontal cortex of macaque monkeys. *J. Comp. Neurol.* 371, 179–207
26. Barbas, H. *et al.* (2011) Sensory pathways and emotional context for action in primate prefrontal cortex. *Biol. Psychiatry* 69, 1133–1139
27. Passingham, R.E. and Wise, S.P. (2015) *The Neurobiology of the Prefrontal Cortex*, Oxford University Press
28. Wallis, J.D. (2012) Cross-species studies of orbitofrontal cortex and value-based decision-making. *Nat. Rev. Neurosci.* 15, 13–19
29. Passingham, R.E. (2021) *Understanding the Prefrontal Cortex: Selective Advantage, Connectivity, and Neural Operations*, Oxford University Press
30. Rolls, E.T. (2023) *Brain Computations and Connectivity*, Oxford University Press
31. Laubach, M. *et al.* (2018) What, if anything, is rodent prefrontal cortex? *eNeuro* 5, 315–333
32. Le Merre, P. *et al.* (2021) The mouse prefrontal cortex: unity in diversity. *Neuron* 109, 1925–1944
33. Rolls, E.T. (2023) Emotion, motivation, decision-making, the orbitofrontal cortex, anterior cingulate cortex, and the amygdala. *Brain Struct. Funct.* 228, 1201–1257
34. Saleem, K.S. *et al.* (2008) Complementary circuits connecting the orbital and medial prefrontal networks with the temporal, insular, and opercular cortex in the macaque monkey. *J. Comp. Neurol.* 506, 659–693
35. Cavada, C. *et al.* (2000) The anatomical connections of the macaque monkey orbitofrontal cortex. A review. *Cereb. Cortex* 10, 220–242
36. Dang, S. *et al.* (2024) Modality-specific and modality-general representations of subjective value in frontal cortex. *Commun. Biol.* 7, 1–19
37. Jang, S.H. and Choi, E.B. (2022) Evaluation of structural neural connectivity between the primary auditory cortex and cognition-related brain areas using diffusion tensor tractography in 43 normal adults. *Med. Sci. Monit.* 28, e936131
38. Wu, Y. *et al.* (2016) Subcomponents and connectivity of the inferior fronto-occipital fasciculus revealed by diffusion spectrum imaging fiber tracking. *Front. Neuroanat.* 10, 210920
39. Saleem, K.S. *et al.* (2014) Subdivisions and connectional networks of the lateral prefrontal cortex in the macaque monkey. *J. Comp. Neurol.* 522, 1641–1690
40. Wang, P.Y. *et al.* (2020) Transient and persistent representations of odor value in prefrontal cortex. *Neuron* 108, 209–224
41. Howard, J.D. *et al.* (2015) Identity-specific coding of future rewards in the human orbitofrontal cortex. *Proc. Natl. Acad. Sci. U. S. A.* 112, 5195–5200
42. Eldridge, M.A.G. *et al.* (2015) Disruption of relative reward value by reversible disconnection of orbitofrontal and rhinal cortex using DREADDs in rhesus monkeys. *Nat. Neurosci.* 19, 37–39
43. Ballesta, S. *et al.* (2022) Orbitofrontal cortex contributes to the comparison of values underlying economic choices. *Nat. Commun.* 13, 4405
44. Rudebeck, P.H. *et al.* (2013) Effects of amygdala lesions on reward-value coding in orbital and medial prefrontal cortex. *Neuron* 80, 1519–1531
45. Ogawa, A. *et al.* (2022) Hypothalamic interaction with reward-related regions during subjective evaluation of foods. *Neuroimage* 264, 119744
46. Bracht, T. *et al.* (2021) The role of the orbitofrontal cortex and the nucleus accumbens for craving in alcohol use disorder. *Transl. Psychiatry* 11, 267
47. Alikaya, A. *et al.* (2017) Reward and value coding by dopamine neurons in non-human primates. *J. Neural Transm.* 125, 565–574
48. Wang, F. *et al.* (2020) Interactions between human orbitofrontal cortex and hippocampus support model-based inference. *PLoS Biol.* 18, e3000578
49. Waskom, M.L. and Wagner, A.D. (2017) Distributed representation of context by intrinsic subnetworks in prefrontal cortex. *Proc. Natl. Acad. Sci. U. S. A.* 114, 2030–2035
50. Ferrari-Toniolo, S. and Schultz, W. (2023) Reliable population code for subjective economic value from heterogeneous neuronal signals in primate orbitofrontal cortex. *Neuron* 111, 3683–3696
51. Enel, P. *et al.* (2021) Heterogeneous value coding in orbitofrontal populations. *Behav. Neurosci.* 135, 245–254
52. Rich, E.L. and Wallis, J.D. (2016) Decoding subjective decisions from orbitofrontal cortex. *Nat. Neurosci.* 19, 973–980
53. Averbeck, B. and O'Doherty, J.P. (2021) Reinforcement-learning in fronto-striatal circuits. *Neuropsychopharmacology* 47, 147–162
54. Spellman, T. *et al.* (2015) Hippocampal-prefrontal input supports spatial encoding in working memory. *Nature* 522, 309–314
55. Thayer, D.D. and Sprague, T.C. (2023) Feature-specific salience maps in human cortex. *J. Neurosci.* 43, 8785–8800
56. Yan, Y. *et al.* (2018) Bottom-up saliency and top-down learning in the primary visual cortex of monkeys. *Proc. Natl. Acad. Sci. U. S. A.* 115, 10499–10504
57. Zhang, W. *et al.* (2022) Reward salience but not spatial attention dominates the value representation in the orbitofrontal cortex. *Nat. Commun.* 13, 6306
58. Xie, Y. *et al.* (2018) Covert shift of attention modulates the value encoding in the orbitofrontal cortex. *eLife* 7, e31507
59. Watson, P. *et al.* (2019) Prioritizing pleasure and pain: attentional capture by reward-related and punishment-related stimuli. *Curr. Opin. Behav. Sci.* 26, 107–113
60. Moorman, D.E. and Aston-Jones, G. (2014) Orbitofrontal cortical neurons encode expectation-driven initiation of reward-seeking. *J. Neurosci.* 34, 10234–10246
61. Huang, H. *et al.* (2024) Attentional control influence habituation through modulation of connectivity patterns within the prefrontal cortex: insights from stereo-EEG. *Neuroimage* 294, 120640
62. Namboodiri, K. *et al.* (2021) Relative salience signaling within a thalamo-orbitofrontal circuit governs learning rate. *Curr. Biol.* 31, 5176–5191
63. Yang, A.I. *et al.* (2021) The what and when of olfactory working memory in humans. *Curr. Biol.* 31, 4499–4511
64. Yu, L. *et al.* (2021) The causal role of auditory cortex in auditory working memory. *eLife* 10, e64457
65. Haegens, S. *et al.* (2010) Somatosensory working memory performance in humans depends on both engagement and disengagement of regions in a distributed network. *Hum. Brain Mapp.* 31, 26–35
66. Liebe, S. *et al.* (2012) Theta coupling between V4 and prefrontal cortex predicts visual short-term memory performance. *Nat. Neurosci.* 15, 456–462
67. Collins, A.G.E. and Frank, M.J. (2018) Within- and across-trial dynamics of human EEG reveal cooperative interplay between reinforcement learning and working memory. *Proc. Natl. Acad. Sci. U. S. A.* 115, 2502–2507
68. Hénaff, O.J. *et al.* (2020) Representation of visual uncertainty through neural gain variability. *Nat. Commun.* 11, 2513
69. Bell, A.H. *et al.* (2016) Encoding of stimulus probability in macaque inferior temporal cortex. *Curr. Biol.* 26, 2280–2290
70. Tsumura, K. *et al.* (2022) Perceptual uncertainty alternates top-down and bottom-up fronto-temporal network signaling during response inhibition. *J. Neurosci.* 42, 4567–4579
71. Balsdon, T. *et al.* (2021) Separable neural signatures of confidence during perceptual decisions. *eLife* 10, e68491
72. Li, Y. *et al.* (2016) The neural dynamics of reward value and risk coding in the human orbitofrontal cortex. *Brain* 139, 1295–1309
73. Masset, P. *et al.* (2020) Behavior- and modality-general representation of confidence in orbitofrontal cortex. *Cell* 182, 112–126

74. Cortese, A. *et al.* (2020) Unconscious reinforcement learning of hidden brain states supported by confidence. *Nat. Commun.* 11, 4429
75. Moneta, N. *et al.* (2023) Task state representations in vmPFC mediate relevant and irrelevant value signals and their behavioral influence. *Nat. Commun.* 14, 3156
76. Niv, Y. (2019) Learning task-state representations. *Nat. Neurosci.* 22, 1544–1553
77. Tolman, E.C. (1948) Cognitive maps in rats and men. *Psychol. Rev.* 55, 189–208
78. O'Keefe, J. and Nadel, L. (1978) *The Hippocampus as a Cognitive Map*, Clarendon Press
79. Behrens, T.E.J. *et al.* (2018) What is a cognitive map? Organizing knowledge for flexible behavior. *Neuron* 100, 490–509
80. De Martino, B. and Cortese, A. (2023) Goals, usefulness and abstraction in value-based choice. *Trends Cogn. Sci.* 27, 65–80
81. Sleezer, B.J. *et al.* (2016) Rule encoding in orbitofrontal cortex and striatum guides selection. *J. Neurosci.* 36, 11223–11237
82. Baram, A.B. *et al.* (2021) Entorhinal and ventromedial prefrontal cortices abstract and generalize the structure of reinforcement learning problems. *Neuron* 109, 713–723
83. Garvert, M.M. *et al.* (2023) Hippocampal spatio-predictive cognitive maps adaptively guide reward generalization. *Nat. Neurosci.* 26, 615–626
84. Koster, R. *et al.* (2018) Big-loop recurrence within the hippocampal system supports integration of information across episodes. *Neuron* 99, 1342–1354
85. Soni, A. and Frank, M.J. (2025) Adaptive chunking improves effective working memory capacity in a prefrontal cortex and basal ganglia circuit. *eLife* 13, RP97894
86. Yoshida, K. and Toyoizumi, T. (2025) A biological model of nonlinear dimensionality reduction. *Sci. Adv.* 11, eadp9048
87. Lake, B.M. and Baroni, M. (2023) Human-like systematic generalization through a meta-learning neural network. *Nature* 623, 115–121
88. Boorman, E.D. *et al.* (2021) The orbital frontal cortex, task structure, and inference. *Behav. Neurosci.* 135, 291–300
89. Tan, L. *et al.* (2025) The medial and lateral orbitofrontal cortex jointly represent the cognitive map of task space. *Commun. Biol.* 8, 1–11
90. Elston, T.W. and Wallis, J.D. (2025) Context-dependent decision-making in the primate hippocampal–prefrontal circuit. *Nat. Neurosci.* 28, 374–382
91. Banerjee, A. *et al.* (2020) Value-guided remapping of sensory cortex by lateral orbitofrontal cortex. *Nature* 585, 245–250
92. Antono, J.E. *et al.* (2023) Distinct patterns of connectivity between brain regions underlie the intra-modal and cross-modal value-driven modulations of the visual cortex. *J. Neurosci.* 43, 7361–7375
93. Hartikainen, K.M. *et al.* (2012) Orbitofrontal cortex biases attention to emotional events. *J. Clin. Exp. Neuropsychol.* 34, 588–597
94. Antono, J.E. *et al.* (2022) Value-driven modulation of visual perception by visual and auditory reward cues: the role of performance-contingent delivery of reward. *Front. Hum. Neurosci.* 16, 1062168
95. Zhang, P. *et al.* (2018) High reward enhances perceptual learning. *J. Vis.* 18, 11
96. Liu, D. *et al.* (2020) Orbitofrontal control of visual cortex gain promotes visual associative learning. *Nat. Commun.* 11, 2784
97. Macedo-Lima, M. *et al.* (2024) Orbitofrontal cortex modulates auditory cortical sensitivity and sound perception in Mongolian gerbils. *Curr. Biol.* 34, 3354–3366
98. Wang, D. *et al.* (2024) Orbitofrontal control of the olfactory cortex regulates olfactory discrimination learning. *J. Physiol.* 602, 7003–7026
99. Chaumon, M. *et al.* (2014) Visual predictions in the orbitofrontal cortex rely on associative content. *Cereb. Cortex* 24, 2899–2907
100. Kam, J.W.Y. *et al.* (2018) Orbitofrontal damage reduces auditory sensory response in humans. *Cortex* 101, 309–312
101. Qin, N. *et al.* (2021) Reward-driven attention alters perceived salience. *J. Vis.* 21, 7
102. Roelfsema, P.R. *et al.* (2010) Perceptual learning rules based on reinforcers and attention. *Trends Cogn. Sci.* 14, 64–74
103. Zhang, N. and Xu, N. long (2022) Reshaping sensory representations by task-specific brain states: toward cortical circuit mechanisms. *Curr. Opin. Neurobiol.* 77, 102628
104. Anderson, B.A. (2019) Neurobiology of value-driven attention. *Curr. Opin. Psychol.* 29, 27–33
105. Taschereau-Dumouchel, V. *et al.* (2021) Conducting decoded neurofeedback studies. *Soc. Cogn. Affect. Neurosci.* 16, 838–848
106. Howard, J.D. *et al.* (2020) Targeted stimulation of human orbitofrontal networks disrupts outcome-guided behavior. *Curr. Biol.* 30, 490–498
107. Jeon, H.A. and Friederici, A.D. (2017) What does "being an expert" mean to the brain? functional specificity and connectivity in expertise. *Cereb. Cortex* 27, 5603–5615
108. Brosch, M. *et al.* (2011) Representation of reward feedback in primate auditory cortex. *Front. Syst. Neurosci.* 5, 5
109. Chikazoe, J. *et al.* (2014) Population coding of affect across stimuli, modalities and individuals. *Nat. Neurosci.* 17, 1114–1122
110. Kaskan, P.M. *et al.* (2016) Learned value shapes responses to objects in frontal and ventral stream networks in macaque monkeys. *Cereb. Cortex* 27, 2739–2757
111. Suthaharan, P. *et al.* (2024) Lesions to the mediodorsal thalamus, but not orbitofrontal cortex, enhance volatility beliefs linked to paranoia. *Cell Rep.* 43, 114355
112. Rudebeck, P.H. *et al.* (2013) Prefrontal mechanisms of behavioral flexibility, emotion regulation and value updating. *Nat. Neurosci.* 16, 1140–1145
113. Tsai, M.C. *et al.* (2024) Hierarchy of prediction errors shapes the learning of context-dependent sensory representations. *bioRxiv* Published October 1st 2024. https://doi.org/10.1101/2024.09.30.615819
114. Wang, J.X. *et al.* (2018) Prefrontal cortex as a meta-reinforcement learning system. *Nat. Neurosci.* 21, 860–868
115. Hattori, R. *et al.* (2023) Meta-reinforcement learning via orbitofrontal cortex. *Nat. Neurosci.* 26, 2182–2191
116. Koops, E.A. *et al.* (2020) Cortical tonotopic map changes in humans are larger in hearing loss than in additional tinnitus. *J. Neurosci.* 40, 3178–3185
117. Janko, D. *et al.* (2022) Somatotopic mapping of the fingers in the somatosensory cortex using functional magnetic resonance imaging: a review of literature. *Front. Neuroanat.* 16, 866848
118. Alvarez, I. *et al.* (2021) Human primary visual cortex shows larger population receptive fields for binocular disparity-defined stimuli. *Brain Struct. Funct.* 226, 2819–2838
119. Li, Q. *et al.* (2024) Representations and generalization in artificial and brain neural networks. *Proc. Natl. Acad. Sci. U. S. A.* 121, e2311805121
120. Mcdannald, M.A. *et al.* (2012) Model-based learning and the contribution of the orbitofrontal cortex to the model-free world. *Eur. J. Neurosci.* 35, 991–996
121. Mnih, V. *et al.* (2015) Human-level control through deep reinforcement learning. *Nature* 518, 529–533
122. Yamins, D.L.K. and DiCarlo, J.J. (2016) Using goal-driven deep learning models to understand sensory cortex. *Nat. Neurosci.* 19, 356–365
123. Cross, L. *et al.* (2021) Using deep reinforcement learning to reveal how the brain encodes abstract state-space representations in high-dimensional environments. *Neuron* 109, 724–738
124. Song, H.F. *et al.* (2017) Reward-based training of recurrent neural networks for cognitive and value-based tasks. *eLife* 6, e21492
125. Song, Y. *et al.* (2024) Inferring neural activity before plasticity as a foundation for learning beyond backpropagation. *Nat. Neurosci.* 27, 348–358
126. Botvinick, M. *et al.* (2019) Reinforcement learning, fast and slow. *Trends Cogn. Sci.* 23, 408–422
127. Bellemare, M.G. *et al.* (2017) A distributional perspective on reinforcement learning. In *34th International Conference on Machine Learning, ICML 2017* (1)
128. Muller, T.H. *et al.* (2024) Distributional reinforcement learning in prefrontal cortex. *Nat. Neurosci.* 27, 403–408
129. Majumdar, G. *et al.* (2023) Emotion dynamics as hierarchical Bayesian inference in time. *Cereb. Cortex* 33, 3750–3772