

# The Orbital Frontal Cortex, Task Structure, and Inference

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The orbital frontal cortex (OFC) has long been linked to goal-directed, flexible behaviors. Recent evidence suggests the OFC plays key roles in representing the abstracted structure of task spaces, and using this representation for flexible inferences during both learning and choice. Here, we review convergent evidence from studies in animal models and humans in support of this view. We begin by considering early accounts of OFC function, then discuss how more recent evidence supports theories that have re-cast OFC's function as representing the structure of a task or environment for flexible inference. Finally, we turn to neural recording studies that provide insights into the underlying representations and computations the OFC may implement in coordination with other brain areas.

**Keywords:** orbital frontal cortex, task structure, inference, cognitive map

## A Brief History of OFC Function in Contingent Learning

Early accounts of the orbital frontal cortex's (OFC) function emphasized response inhibition (Chudasama & Robbins, 2003; Iversen & Mishkin, 1970; Jones & Mishkin, 1972; Winstanley et al., 2003) and emotional processing (or "somatic markers"; Bechara et al., 2000; Kringelbach & Rolls, 2004; Rolls et al., 1994). These and related accounts were largely based on patterns of deficits following damage to the OFC and neighboring regions, such as ventromedial prefrontal cortex (vmPFC), following "naturally occurring" lesions in humans and total experimental lesions to the OFC in monkeys and rodents on two classical tasks: Reversal learning and reinforcer devaluation (Figure 1).

In reversal learning studies, these lesions produced perseverative choices following reversal of the identities of the more rewarding and less rewarding cues (Bechara et al., 1997; Dias et al., 1996; Schoenbaum et al., 2002). This inflexibility was first attributed to an insensitivity to the affective or visceral consequences of negative outcomes (Bechara et al., 2000; Kringelbach & Rolls, 2004) or an inability to inhibit previously rewarded responses (Chudasama & Robbins, 2003; Jones & Mishkin, 1972). More recent evidence has shown that animals with OFC lesions are equally or more likely to inhibit previously rewarded choices and switch responses under many circumstances (Chudasama et al., 2007; Riceberg et al., 2012; Walton et al., 2010). Furthermore, OFC neurons do not fire when inhibitory control needs to be implemented, but rather to predictive cues and in anticipation of their outcomes, and at the time of valenced

feedback (Kennerley et al., 2009; Rich & Wallis, 2016; Saez et al., 2018; Schoenbaum & Roesch, 2005). Moreover, OFC neurons fire in similar proportions to positively and negatively-valenced outcomes when they are equally informative for future behavioral adjustments (Morrison & Salzman, 2009; Rushworth et al., 2011). More recent evidence suggests it may be the most lateral OFC/ventrolateral prefrontal subdivision (area 47/12, Brodmann & Garey, 2006; Walker, 1940) in particular that is most critical for reversal learning (Noonan et al., 2017; Rudebeck et al., 2013, 2017; Rushworth et al., 2011), although a recent study also found that theta, but not beta, frequency-locked stimulation of centro-lateral OFC (area 13) causally disrupted contingent learning behavior. More recent accounts have instead suggested such deficits may arise from impairments to stimulus value updating and credit assignment (Rushworth et al., 2011), value updating (Murray & Rudebeck, 2018), or a representation of one's position in a "task space" (Wilson, Takahashi, Schoenbaum, & Niv). See (Murray & Rudebeck, 2018; Rushworth et al., 2011; Stalnaker et al., 2015; Wilson et al., 2014) for comprehensive reviews of these and other theories that discuss alternative perspectives on the role of OFC in contingent learning and other functions, which are beyond the scope of this review.

## Reconsidering OFC Function in Light of "Task Structure"

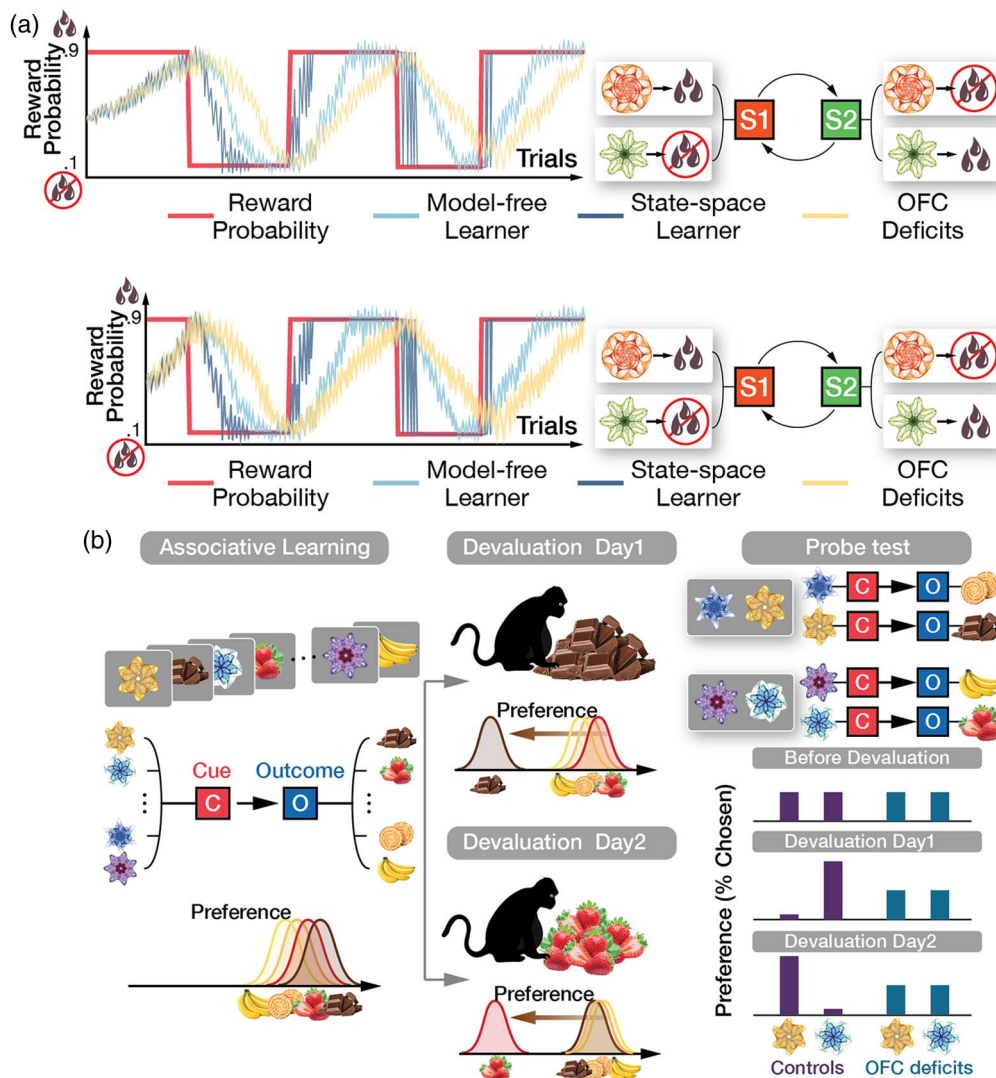
One particularly general theory of OFC function, termed the "cognitive map of task space" (Wilson et al., 2014), has proposed that the role of the OFC in reversal learning and other tasks can be understood by considering the behaviorally-relevant "task space" the animal might need to represent to solve a particular task. In the case of reversal learning tasks, the animal's "task space" would entail the choice stimuli (e.g., visual or odor cues), beliefs about associations between stimuli and outcomes, outcome states (e.g., positive and negative reinforcement outcomes following a specific choice), and, importantly, the inferred task structure (Figure 1). Here, the task structure refers to the statistical relationships between states or entities (e.g., objects, people) involved in the task and how

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**Figure 1***Task Structure in Classic OFC-Dependent Tasks and the Real World*

**Note.** (A) Example reversal learning task. Left: example reversal learning task. True reward probability (red), a standard model-free learner [e.g., a Q-learning algorithm with a RW update rule (Rescorla and Wagner, 1972)] with a fixed learning rate estimates (light blue), a state-space learner's estimates that infers the latent state (dark blue), and idealized OFC lesion animals' choices of the better option are shown. The standard model-free learner gradually updates its value estimate after each reversal, with a rate of updating that does not change with experience of reversals. By contrast, the state-space learner (e.g., Hampton et al., 2006) that jointly infers the reward probability and the hidden state (S1 is the current high reward state) learns more quickly following a reversal and this rate increases with more reversals because it benefits from explicitly estimating the reversal likelihood. Following lateral OFC lesions, animals are impaired at reversing their choice behavior and rapidly acquiring the new association. Right: illustration of the task structure of the state inference problem in a reversal learning task. In State 1 (S1) stimulus A (B) leads to reward with high (low) probability and this reverses back and forth to State 2 (S2), where these contingencies are reversed, after a predictable number of trials. (B) Example reward devaluation task. During the associative learning phase (left), four cues are uniquely associated with four distinct rewards, ideally of similar value (relative preference). During the devaluation phase (middle), one reward is specifically devalued by feeding it to the animal until they reach satiety. In this example, a different reward is devalued on different days. During the probe test (right), cues that have been compared before are pit against one another for binary choices. Healthy control animals choose the non-devalued cues over the de-valued cues (bottom right), demonstrating goal-directed choices. Animals with lateral OFC damage choose at chance but still show normal preferences when presented with choices between the actual foods, suggesting their relative preference and ability to choose are not altered. Task structure is illustrated with cue (C) → outcome (O) pairings. (C) Example task structures humans and other animals face in the real world. Cyclic relationships between seasons with inverse relationships across Northern and Southern hemispheres (left), "buy" and "sell" states investors face in the stock market (middle), and relationships between people in social hierarchies (right) are shown. Animals can use such structural knowledge to infer new relationships from experienced relationships, thus accelerating learning and promoting behavioral flexibility (shown for the social hierarchy, right). See the online article for the color version of this figure.

Figure 1 (Continued)



they transition over time. Specifically, in most reversal learning paradigms, one high-value option is either deterministically or stochastically rewarded with a high probability and the other is not rewarded or only with a low probability. After learning of these initial contingencies, there is one or more reversals in the identity of the high-value choice option. While this class of tasks has most commonly been modeled computationally using “model-free” learning algorithms that incrementally update stimulus-reward associations using reward prediction errors, such as Rescorla–Wagner (RW; Rescorla & Wagner, 1972) and Pearce–Hall models (Pearce & Hall, 1980), the task has an underlying structure that more recent evidence suggests animals can, and do, learn to exploit.

Reversal tasks can be re-cast as an inference problem in which the animal alternates between two hidden states, one in which stimulus A is better and B is worse, and the reverse (Gershman et al., 2015; Hampton et al., 2006; Figure 1A). The animal’s task, therefore, is to infer in which hidden state it currently is and when this state changes. By tracking the likelihood of a reversal, animals will be more flexible at switching their behavior following unexpected negative outcomes because they have learned the underlying task structure. In line with this prediction, several studies have now shown that models that infer the current hidden state jointly with the reward probabilities better explain behavior than model-free models, including hierarchical Bayesian models that track higher order statistics such as the volatility to dynamically adjust the learning rate, that are agnostic to this task structure (Bartolo & Averbeck, 2020; Boorman et al., 2016; Hampton et al., 2006; Verтеchi et al., 2020). Note that while some model-free formalizations also adjust the learning rate dynamically according to the estimated uncertainty or volatility (Behrens et al., 2007; Nassar et al., 2010), their generative model does not benefit from an understanding the true task structure of the reversal task, and have been shown to be outperformed on reversal learning tasks by models that do (Boorman et al., 2016). This implies that animals are indeed picking up on the underlying task structure and exploiting it for flexible behavior.

The dependence of hidden state inference on the OFC when it requires knowledge of the task structure has recently been demonstrated, even in mice (Verтеchi et al., 2020). Rather than use a classic

reversal task, the authors designed a hidden state foraging task with an asymmetric payout. On each trial mice actively probed “foraging sites” by sampling a port, which stochastically led to a water reward ( $p = .9$ ) for the “good” state but never for the “bad” state ( $p = 0$ ). Critically, the task was designed to be asymmetric such that a single failure to receive reward only provided partial evidence that the “foraging” site had switched, but a single reward provided full certainty that the sampled site was rewarding. Thus, only a single reward carried full information about the hidden state (the rewarded site is the “good” state). Unlike most learning tasks, this asymmetry implies that multiple rewards at the same foraging site should not have any bearing on when to infer a switch has occurred after a failure, though they would increase the model-free value of the site. Using a series of behavioral analyses, Verтеchi et al. showed that both human and mouse behavior reflected an understanding of this task structure (though mice were unsurprisingly much slower to learn the structure). In mice, optogenetic inhibition of OFC selectively impaired such inference-based decisions that relied on an understanding of the task structure, leaving animals “stimulus-bound” such that, unlike control animals, their switching behavior depended on the number of rewards obtained before obtaining negative outcomes. Notably, anterior cingulate cortex (ACC) inactivation delayed leaving decisions, consistent with a role in determining when to adapt behavior (Boorman, Rushworth, & Behrens, 2013; Hayden et al., 2011; Karlsson et al., 2012; Kolling et al., 2012, 2016), but did not alter indices of inference behavior, highlighting a potentially specialized role for OFC.

In a similar vein, patterns of monkey choices on stochastic multi-arm “bandit” tasks following OFC lesions have revealed impairments following reversals and even during initial acquisition of contingencies that can be elegantly accounted for by a specific deficit in precise credit assignment, which in turn depends on knowledge of the task structure (Walton et al., 2010). The deficit in the precise attribution of contingent outcomes to their causal choices unmasked a tendency to attribute outcomes to the recent average history of choices, known as the “spread of effect” (Thorndike, 1933). While this spreading mechanism is sufficient for learning when contingencies are stable, it will fail when they change or are sufficiently uncertain. But how does a foraging animal



know which choices are causal? The contingent relationship between specific choices and their outcomes embedded in the task structure is likely to be learned by the animal through extensive training, by forming what was originally called a “learning set” (Harlow, 1949). One intriguing suggestion (Seo & Lee, 2010; Stalnaker et al., 2015; Walton et al., 2010) is that precise credit assignment requires knowledge of the task structure—that each outcome is only contingent on the latest choice, but not previous choices (i.e., each choice is statistically independent). Without an accurate representation of this task structure, the animal will attribute outcomes using the **recency-weighted average history of choices** (Walton et al., 2010). Collectively, the deficits in these studies can be understood as reflecting an inability to infer or use a model of the task structure for adaptive learning.

The view that the OFC represents the abstracted structure of the task space can also potentially account for the role of OFC in other flexible, goal-directed behaviors. Another classic OFC-dependent task across species is reinforcer devaluation (Baxter et al., 2000; Gallagher et al., 1999; Howard et al., 2020; Izquierdo et al., 2004; Kaplan et al., 2012; Murray et al., 2015; Pickens et al., 2003; Rudebeck et al., 2013; West et al., 2011). This task was first used as early as the 1940s as one of several paradigms that supported the idea that rats form and use “cognitive maps” of the environment for goal-directed behaviors (Tolman, 1948; Figure 1B). Notably, monkey OFC lesions both before the satiation procedure that updates the value of the sated reward type (Murray et al., 2015), and after the satiation procedure (Murray et al., 2015; West et al., 2011) **impair such goal-directed choices, implying that OFC is necessary not only for updating the value of the reinforcer during devaluation, but for the use of a predictive model of the associations between specific choices and specific likely outcomes to construct the updated value in the animal’s new satiated state.** Here, the most critical areas appear to be in central-lateral subdivisions of OFC (areas 11 and 13; Murray et al., 2015; West et al., 2011), with a potential dissociation such that area 13 is critical for value updating but area 11 for choices based on the updated value (Murray et al., 2015). This deficit at choice could also potentially be ascribed to abolishing a model of the task structure—that is, that choice of some cue A leads to a specific outcome X, and a different cue B to a distinct outcome Y, and to impairments in on-the-fly construction of expected outcomes (including their identities, sensory features, and current values) using this task structure in new situations. This is because the choice had never been made in the satiety-induced state before, meaning the new expected outcome value is likely constructed (Figure 1B).

What remains unclear from these studies is the precise role(s) to be attributed to the OFC. **Does the OFC store and represent the abstracted task structure locally, or is this structure stored elsewhere, such as the hippocampal formation, and accessed to guide behavior under certain circumstances?** Furthermore, does the OFC play a role in computing inferred information during learning and choice, and, if so, under what circumstances?

### OFC Codes for the Behaviorally-Relevant Task Space

To shed light onto these questions, we turn to neural recording studies that elucidate the nature of OFC coding. Convergent evidence across species has identified neural representations of behaviorally relevant task variables, including hidden states, that are critical components of the task space for both contingent learning

and goal-directed choice. For instance, a memory of the past choice can be decoded from monkey OFC neurons specifically at the time reinforcement outcomes are delivered, precisely when credit needs to be assigned (Tsujimoto et al., 2009). Likewise, OFC inactivation in rats causes abnormal dopaminergic reward prediction error signals measured in ipsilateral VTA that can be elegantly accounted for by the loss of choice memory necessary for appropriate credit assignment (Takahashi et al., 2011). Using fMRI in humans, a similar role for human lateral OFC in precise credit assignment has likewise been identified when subjects attributed outcomes either to a particular person’s ability or to the situation, in order to update future predictions (Boorman, O’Doherty, et al., 2013). Another study in humans directly investigated contingent learning and spread of effect learning in the same task (Jocham et al., 2016). This study found both types of learning could be measured in humans, were uncorrelated behaviorally between individuals, and were neurally dissociable. Specifically, they identified BOLD effects for contingent but not non-contingent (or “free”) rewards of equal value, whose distinction depended on instructed knowledge of the task structure—namely, that the contingent but not non-contingent reward would be delivered following a 3s delay. Importantly, during this 3s window another choice would frequently have been made and a non-contingent free reward would frequently have been delivered. The extent to which subjects appropriately attributed credit for contingent over free rewards to their causal over non-causal choices was associated with greater lateral OFC activation to contingent rewards across individuals (in putative areas 11 and 13). In addition to such univariate outcome signals, pattern similarity in lateral OFC has been shown to reflect distributions over potential latent causes during causal inferences, consistent with a role in reactivating hidden causes (Chan et al., 2016). Furthermore, during reversal learning tasks with distinct outcome identities, expected outcome identities can be decoded from BOLD activation patterns in OFC during cue presentation, and moreover, learning update signals about the expected outcome type (sometimes referred to as “identity prediction errors”) are reflected in both OFC and dopaminergic ventral midbrain BOLD activity at feedback (Boorman et al., 2016; Howard & Kahnt, 2018; Suarez et al., 2019). In the context of these reversal learning tasks, update signals at the time of feedback not only revise the stimulus-outcome associations, but also whether to infer the currently believed hidden state is still in play or has changed (Figure 1A). Whether these OFC learning signals measured with BOLD reflect local signaling or input to OFC remains an important open question. Finally, recent evidence suggests that hippocampal representations of the latent context or state provide a theta-locked input to the lateral OFC to guide appropriate expectations for learning and decision-making (Knudsen & Wallis, 2020; Wikenheiser et al., 2017), putatively through direct connections from hippocampus to OFC (Barbas & Blatt, 1995).

In the context of decision-making, OFC neurons have been shown to independently signal the expected or inferred outcome identity (e.g., reward flavor) and value of specific rewards (Hunt et al., 2018; McDannald et al., 2014; Padoa-Schioppa & Assad, 2006, 2008; Stalnaker et al., 2014). Using an unblocking paradigm, one study paired odor cues with a specific reward identity (e.g., chocolate milk) of a specific amount (“value”; McDannald et al., 2014). Subsequently, a second cue was presented after the first cue in either of three conditions: The identity and amount

predicted by the original cue remained the same, thus blocking the new cue (blocking condition), the flavor or identity was changed to a similarly preferred outcome (e.g., vanilla; identity unblocking), or the identity remained the same but the amount was changed (value unblocking). Behavioral analyses showed that conditioned responses were blocked to the new cue in the blocking condition but were acquired in the two unblocking conditions. Critically, lateral OFC neurons acquired responses to the value-unblocked and identity-unblocked cues, or both, with a subpopulation responding exclusively to the unblocked cues. These OFC responses are consistent with the formation of a new inferred state representation for the unblocked cues, which would alter the task space.

Suppression and pattern-based analyses designed to measure representational content from human fMRI data have likewise shown that expected and inferred outcome identity (Howard et al., 2015; Howard & Kahnt, 2017; Klein-Flügge et al., 2013; Pauli et al., 2019), stimulus-outcome associations (Klein-Flügge et al., 2013; McNamee et al., 2015), and value of specific rewards (e.g., food and trinkets; McNamee et al., 2013; Pauli et al., 2019) can be identified in lateral OFC. Notably, abstracted values that generalize over attributes and outcomes (e.g., different reward types and attributes) appear to be preferentially encoded and represented in medial OFC/vmPFC, at least in humans (Chib et al., 2009; Clithero & Rangel, 2014; Howard & Kahnt, 2017; McNamee et al., 2013), a region also implicated in the comparison of values during goal-directed decisions (Boorman et al., 2009; Hunt et al., 2012, 2018; Lim et al., 2011; Noonan et al., 2010; Rudebeck & Murray, 2011; Rushworth et al., 2011; Strait et al., 2014). Furthermore, the motivational significance of predicted outcomes modulates many of these OFC expectation signals, highlighting its role in motivated behavior. Following reward devaluation (see Figure 1), lateral OFC neuronal activity (Critchley & Rolls, 1996a, 1996b) and human BOLD activity in medial and lateral OFC (Gottfried et al., 2003; Howard & Kahnt, 2017; Valentin et al., 2007) to cues predicting previously valued rewards diminish following outcome-specific devaluation, consistent with some role for motivational value in determining OFC engagement.

Several studies have highlighted a prominent representation of value or reward expectation, both in individual OFC neurons and the OFC population code (Farovik et al., 2015; Hunt et al., 2018; Kennerley et al., 2011; Padoa-Schioppa & Assad, 2006, 2008; Rich & Wallis, 2016; Zhou et al., 2019), a representation that has been consistently identified in monkey area 13 (e.g., Hunt et al., 2018; Padoa-Schioppa & Assad, 2006, 2008; Rich & Wallis, 2016). Yet when animals and humans need to remember previous states (e.g., abstract rules or stimuli) or use multiple attributes for optimal choices, those value-independent but behaviorally relevant components of the task space are also encoded or represented in OFC in rats (Roesch et al., 2006; Sadacca et al., 2018; Zhou et al., 2019, 2020), monkeys (Blanchard et al., 2015; O'Neill & Schultz, 2010; Watson & Platt, 2012), and humans (Saez et al., 2018; Schuck et al., 2016; Wang et al., 2020), with the behaviorally relevant hidden states decodable from human OFC (Schuck et al., 2016). These generally convergent findings suggest that the lateral OFC contains a rich representation of behaviorally or motivationally relevant components of the task space, with value constituting one of several variables represented.

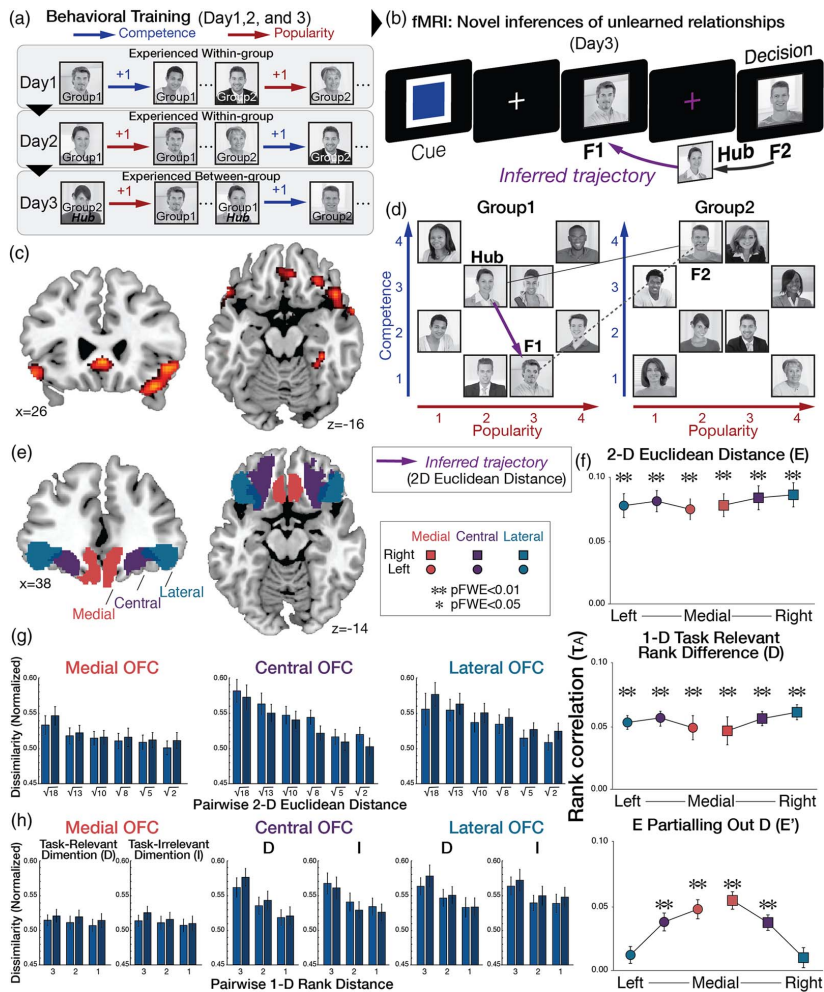
## A Cognitive Map for Flexible Inferences in OFC

While there is mounting evidence that those behaviorally relevant or motivationally salient components of the task space, including past stimuli or choices, abstract rules, and future expected outcome attributes, are represented in OFC for both learning and choice, we were interested in whether there is evidence in OFC coding for a “cognitive map,” consisting of the *relationships* between states or entities (people or things) that form the underlying task structure, and whether the OFC may use such a representation to perform inference computations.

To shed light on these and related questions, we designed two human fMRI studies (Park, Miller, & Boorman, 2020; Park, Miller, Nili, et al., 2020). Subjects learned two (unseen) eight-person social hierarchies organized along two abstract dimensions: competence and popularity. Each hierarchy dimension was learned piecemeal from the outcomes of choices about the higher rank person between pairs of only one rank-level difference on a single dimension, with each dimension learned on a different day (Figure 2A). Unbeknownst to participants, the individuals could be arranged in a latent 2D space (though they did not *have* to be), which can be conceptualized as a central component of the hidden task structure. On day 3 subjects learned from select comparisons involving “hubs” that could be used to bridge the two hierarchies for the first time and potentially combine them into a single 2D hierarchy. Finally, during fMRI subjects made novel inferences about the relative rank of pairs of people who had never been compared in either dimension, with one coming from each group (Figure 2B). Although only one social dimension was behaviorally relevant for these decisions, the similarity between multivariate activity patterns (measured with RSA) in lateral, central, and medial OFC [Figure 2E; and also in hippocampus (HC) and entorhinal cortex (EC)] were linearly related to the Euclidean distance between people in the reconstructed 2D space, such that more proximal people were represented progressively more similarly (Figure 2F-H). This finding suggests these areas spontaneously reconstruct an abstracted cognitive map of the hidden 2D relational task structure. Furthermore, behavioral and neural analyses indicated that subjects retrieved the relevant latent hub to enable novel inferences between groups. Specifically, both decision response times and decision-related univariate activity in lateral OFC (and also in vmPFC and EC; Figure 2C) reflected the Euclidean distance of direct inferred vectors over the reconstructed 2-D space to the retrieved latent hub (Figure 2D).

Building on these findings, in a second study (Park, Miller, & Boorman, 2020), subjects learned a single unseen  $4 \times 4$  2D social hierarchy comprising 16 “entrepreneurs” through the same training procedure (see Figure 2A), but for the fMRI task subjects were instead asked to make novel decisions about which of two potential partners would make a better collaborator for a given “entrepreneur” (Figure 3). To guide these novel decisions, we hypothesized people would infer direct vectors over the reconstructed 2D cognitive map. We identified grid-like coding (hexagonally symmetric modulation) in EC (where grid cells are commonly found (Hafting et al., 2005), and also in lateral OFC and mPFC, for *inferred* direct trajectories over the reconstructed abstract 2D space during the evaluation of each decision option (Figure 3). This latter finding is consistent with recent demonstrations of grid-like coding in a markedly similar set of brain areas, including lateral OFC, in a study that required subjects to “navigate” through a continually morphing visual 2D

**Figure 2**  
*Cognitive Maps and Inferences in OFC*

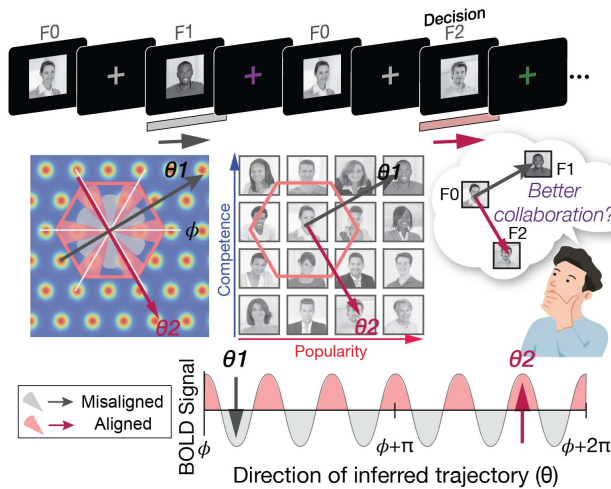


**Note.** (A) Behavioral training procedure over 3 days (Park, Miller, Nili, et al., 2020). On days 1–2, subjects learned the relative status of two groups of eight “entrepreneurs” on two independent social dimensions (competence and popularity) through feedback-based binary choices, with only one dimension learned per day for each group (order counterbalanced). Then on day 3, they learned the relative status of select hubs that linked the two groups of eight through binary comparisons. All learned comparisons were of 1 rank level difference only. (B) fMRI experimental task. A cue’s color indicated the relevant dimension (popularity or competence) for the current trial, followed by two faces presented sequentially, each coming from a different group. The figure illustrates the latent hub hypothesized to be used for novel inferences. (C) Axial slice through parametric map of the effect of the Euclidian distance between the retrieved task-relevant hub and the face from its own group (F1) used to guide inference decisions. Images are displayed at  $p < .005$  uncorrected for display purposes. Significant clusters were identified in medial, central, and lateral OFC and bilateral EC (not shown; using whole-brain correction at  $p < .05$  with threshold-free cluster enhancement (Smith & Nichols, 2009)). (D) Illustration of the two 2D hierarchies (groups), each consisting of eight people. Example comparison between F1 and F2 from a single trial, along with the task-relevant hub, and putative trajectory (purple) used for inferences. (E) Illustration of parcellation of OFC into medial, central, and lateral OFC subdivisions, based on their patterns of functional connectivity (Neubert et al., 2015), used in (F)–(H). (F) Mean rank correlation (Kendall’s  $\tau_A \pm \text{SEM}$ ) between representational dissimilarity matrices (RDMs) of the Euclidian distance E (Top) between each face in the true (unseen)  $4 \times 4$  combined hierarchy and neural RDMs at the time of each face presentation in medial, central, and lateral OFC in each hemisphere. The same analysis is shown for an RDM of the task-relevant rank distance D (Middle) and E’, corresponding to E after partialling out the covariance with D (Bottom), indicating that the task-irrelevant dimension (I) also contributed significantly to the effect of E in medial and central but not lateral OFC. (G) Normalized pattern dissimilarity in each OFC subdivision binned according to the Euclidian distance between faces, illustrating a strong linear relationship. (H) The same relationship is plotted with E decomposed into its two components: the task-relevant distance (D) and task-irrelevant distance (I). \*\*  $p < .001$ , Bonferroni-Holm corrected for multiple ROIs. See the online article for the color version of this figure.



**Figure 3**

*Grid-Like Modulation for Inferred Direct Vectors Over the Cognitive Map*



*Note.* Top: Example trial of the “partner selection” task. Subjects’ task was to decide the better collaborator between F1 and F2 for a given “entrepreneur” (F0) based on their combined competence and popularity. These decisions had not been made previously. Middle: We hypothesized subjects would construct vectors over a cognitive map of the  $4 \times 4$  social hierarchy from F0 to F1 and F0 to F2 to guide these novel inferences about the better partner. Bottom: Hypothesized sixfold modulation of the BOLD signal for trajectories aligned compared to misaligned with each subjects’ measured EC grid orientation (see grid field), for hypothesized direct vectors  $\theta_1$  (at F1 presentation) and  $\theta_2$  (at F2 presentation) over the cognitive map. This analysis revealed significant effects in posterior lateral OFC, EC, and mPFC showing hexagonal modulation that was specific to a sixfold periodicity (data not shown; Park, Miller, & Boorman, 2020). See the online article for the color version of this figure.

“bird space” (defined by neck and leg length) to “locate” specific reward outcomes (Christmas tree ornaments; Constantinescu et al., 2016). Taken together, these findings suggest that the OFC represents a cognitive map consisting of the relationships between entities (people or objects) in a multidimensional behaviorally relevant task space, even when the task space is hidden and can only be inferred from piecemeal experiences. Moreover, they suggest that the OFC either computes or accesses direct vectors computed elsewhere over that cognitive map to guide novel inferences.

### Task Structure in OFC Coding During Value-Guided Decision Making

A closer look at the nature of OFC neuronal population coding in some studies suggests a structured representation that is preserved across contexts, including for value coding. For example, during preference-based choices, monkey lateral OFC (area 13) neurons signal the expected or obtained outcome (juice) identity, offer value (amount), and chosen value—key components of this particular task space (Onken et al., 2019; Padoa-Schioppa & Assad, 2006, 2008). As highlighted previously (Behrens et al., 2018), there is a striking conservation of the type of value cell across changes to the “menu” context (i.e., which juices are on offer). In contrast to random mixed selectivity commonly found in prefrontal cortex (Rigotti et al., 2013), OFC cells encoding outcome identity, offer value, and

chosen value largely code for the same variable with the same sign when the menu changes, suggesting that the OFC generalizes across these contexts. In other words, the covariance of OFC neurons in the population is preserved across contexts, thereby reflecting the common task structure in the population code. Indeed, a recent study recording from rat OFC neuronal populations identified categorical clustering of distinct “decision variables” using model-free clustering methods, such as neurons consistently coding for the “integrated decision value” and “confidence” (Hirokawa et al., 2019). These clusters were largely consistent across different periods of the task, exhibiting co-clustering across different task epochs. Based on the above findings in monkeys, this highly structured representation of behaviorally relevant decision variables would be predicted to be preserved across the neuronal population in different instantiations of the task, for example, where the odor mixtures comprised different odorants but the overarching task structure remained preserved (Bao et al., 2019).

### Conclusion

Recent convergent evidence across species points to the value of considering rich multidimensional task spaces with measurable underlying task structures to elucidate OFC function. Explicitly manipulating this underlying abstracted task structure between different contexts, and investigating the initial acquisition of the task structure in the first place, are likely to be fruitful for further revealing the nature of OFC’s role in flexible, goal-directed, and motivated behavior.

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