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An Evolutionarily Adaptive Neural Architecture for Social Reasoning

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Abstract

Recent progress in cognitive neuroscience highlights the involvement of the prefrontal cortex (PFC) in social cognition. Accumulating evidence demonstrates that representations within the lateral PFC enable people to coordinate their thoughts and actions with their intentions to support goal-directed social behavior. Despite the importance of this region in guiding social interactions, remarkably little is known about the functional organization and forms of social inference processed by the lateral PFC. Here we introduce a cognitive neuroscience framework for understanding the inferential architecture of the lateral PFC, drawing upon recent theoretical developments in evolutionary psychology and emerging neuroscience evidence about how this region may orchestrate behavior on the basis of evolutionarily adaptive social norms for obligatory, prohibited, and permissible courses of action.

Architect of the social mind

Evolution has fundamentally shaped the architecture of the mind, producing cognitive and neural mechanisms that are designed to solve adaptive problems encountered by our human ancestors. Throughout evolutionary history, a foremost adaptive challenge for our species was living and interacting with people – learning to select mates, form alliances, and compete for limited resources. Our human ancestors also needed to obey social norms and standard of conduct, as violations of these rules might have restricted the formation of organized social groups and have been severely punished. Accordingly, just as the brain has evolved mechanisms for perception, memory, language, and thought, it is likely that there are also evolutionarily adaptive mechanisms that enable humans to coexist with others.

The neuroscientific study of social cognition reflects the interdisciplinary nature of modern science, with investigators from diverse academic disciplines (including anthropology, evolutionary psychology, social psychology, political science, behavioral economics, and decision neuroscience) exploring the unique social nature of human experience through a multifaceted lens (for recent reviews from the emerging field of *social cognitive neuroscience*, see [1–3]). This interdisciplinary enterprise has made considerable progress in understanding the involvement of the prefrontal cortex (PFC) in social cognition [4–11]. Accumulating evidence indicates that representations within the lateral PFC enable people to

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orchestrate their thoughts and actions in concert with their intentions to support goal-directed social behavior [12–23]. Despite the pivotal role of this region in guiding social interactions, fundamental questions remain concerning the functional organization and forms of social inference processed by the lateral PFC. Here we develop an integrative cognitive neuroscience framework for understanding the inferential architecture of the lateral PFC, reviewing recent theoretical insights from evolutionary psychology and emerging neuroscience evidence to support the importance of this region for orchestrating social behavior on the basis of evolutionarily adaptive social norms.

We begin by reviewing the evolutionary foundations of normative social behavior, surveying contemporary research and theory from evolutionary psychology to suggest that widely shared norms of social exchange are the product of evolutionarily adaptive cognitive mechanisms. We then review the biology, evolution, and ontogeny of the human PFC, and introduce a cognitive neuroscience framework for social reasoning based on evolutionarily adaptive social norms represented within the lateral PFC. Our review examines a broad range of evidence from the social and decision neuroscience literatures demonstrating that social norms for obligatory, prohibited, and permissible behavior are mediated by functionally specialized regions of the lateral PFC. We illustrate how this framework supports the integration and synthesis of a diverse body of neuroscience evidence, and draw conclusions about the role of the lateral PFC in social cognition more broadly, contributing to social knowledge networks by representing widely shared norms of social behavior and providing the foundations for moral, ethical, legal, and political systems of value and belief.

Evolutionary foundations of normative social behavior

Evolutionary psychology has made significant progress in understanding the evolutionary origins of normative social behavior, establishing the central role of *social exchange* in the formation of cooperative human societies. Social exchange promotes the survival of individuals who cooperate for mutual benefit – one providing a benefit to another, conditional on the recipient's providing a benefit in return (for representative findings from behavioral economics, see [24–29]). From our earliest ancestors to present day, social exchange has facilitated access to sustenance, protection and mates, and enabled people to live healthier and longer lives [30,31]. Social exchange interactions are therefore an important and recurrent human activity occurring over a sufficiently long time period for natural selection to have produced specialized cognitive and neural adaptations [32,33]. Evolutionary psychologists have proposed that social exchange embodies cognitive mechanisms designed to promote the survival of our species, representing normative social behavior that develops in all healthy humans and is mediated by evolutionarily adaptive neural systems [34–44].

An empirical case for this proposal has been established on the basis of behavioral and neuroscience research elucidating the role of evolutionary design features in shaping cognitive and neural mechanisms for social exchange [35–39]. Game-theoretic models predict that for social exchange to persist within a species, members of the species must detect cheaters (i.e., individuals who do not reciprocate) and direct future benefits to reciprocators rather than cheaters [40,41]. Accumulating evidence supports this proposal, demonstrating that the mind embodies functionally specialized cognitive mechanisms for detecting cheaters [35–39] that operate according to behavior-guiding principles in the form of a conditional rule: If *X* provides a requested benefit to *Y*, then *Y* will provide a rationed benefit to *X*. A conditional rule expressing this kind of agreement to cooperate is referred to as a *social contract* and represents a normative standard for social behavior (e.g., the normative belief that mutual cooperation is obligatory and cheating prohibited).

A primary method for investigating conditional reasoning about social contracts is Wason's four-card selection task [45]. In the classic version of this task, participants are shown a set of four cards, placed on a table, each of which has a number on one side and a colored patch on the other. The visible faces of the cards show a 3, 8, red, and brown. Participants are then asked which card should be turned over to test the truth of the conditional rule "If a card shows an even number on one face, then its opposite face shows a primary color (red, green, or blue)". Conditional rules representing abstract or descriptive content typically elicit a correct response from only 5 to 30 per cent of participants tested (8 and brown). This finding has been observed even when the rules tested are familiar, or when participants are taught logic or given incentives [35–39,46]. In contrast, when the conditional rule expresses a social contract and a violation represents cheating (e.g., "If she drinks beer then she is 21 years or older"), 65 to 80 per cent of participants generate the correct response (she drinks beer and is not 21 years or older) [35–39]. Cognitive experiments have demonstrated that this improved level of performance is sensitively regulated by the series of variables expected if this were a system optimally designed to reason about obligatory and prohibited forms of social behavior, rather than to support a broader class of inferences [35–39,43,46].

Social contracts therefore represent behavior-guiding principles for evolutionarily adaptive forms of social exchange and are critical for drawing inferences about necessary courses of action concerning socially obligatory or prohibited behavior. From an evolutionary perspective, normative standards for necessary forms of social exchange can be distinguished from a broader class of inferences concerning possible or permissible courses of action. Social norms for (i) *necessary behavior* are central for the organization of society, representing strictly enforced rules for cooperation, the division of labor, and the distribution of resources. In contrast, social norms for (ii) *permissible behavior* are critical for achieving adaptive goals within society, representing non-punishable courses of action that enable individuals to explore opportunities for reward and gain access to available resources [34,36–43]. We propose that evolutionary adaptations for reasoning about necessary (obligatory or prohibited) versus possible (permissible) courses of action have therefore fundamentally shaped the architecture of the mind, producing functionally distinct cognitive and neural mechanisms for reasoning about necessary and possible states of affairs. While cognitive and neural mechanisms for these forms of inference emerged from goal-directed social behavior [34–43], non-social inferences are also shaped by these systems, relying upon an evolutionarily adaptive neural architecture that distinguishes between these two fundamental classes of inference.

We examine the contributions of the human PFC to social reasoning in the following section, introducing a cognitive neuroscience framework for understanding the inferential architecture of the lateral PFC.

Simulation theory of prefrontal cortex function

One of the great mysteries of brain function concerns how coordinated, purposeful behavior arises from neural states. How are people able to orchestrate their thoughts and actions in concert with their intentions to support goal-directed social behavior? An emerging body of evidence suggests that this capacity centrally depends on the PFC, which is particularly important for grouping specific experiences of our interactions with the environment along common themes, that is, as behavior-guiding principles. To this end, our brains have evolved mechanisms for detecting and storing complex relationships between situations, actions, and consequences. By gleaning this knowledge from past experiences, we can develop behavior-guiding principles that allow us to infer which goals are available in similar situations in the future and what actions are likely to bring us closer to them.

Accumulating evidence demonstrates that behavior-guiding principles for social inference operate on the basis of a broadly distributed, hierarchically organized neural architecture (for empirical reviews from neuroscience and psychology, see [5–11,47–49]). It is widely known that experience in the physical and social world activates feature detectors in relevant features maps of the brain (for a review feature maps in vision, see [50]). When a pattern becomes active in a feature map during perception or action, conjunctive neurons, in an association area, capture the pattern for later cognitive use [5–11,47–49].

We propose that behavior-guiding principles for social inference are mediated by higher-order association areas localized within the lateral PFC. Decades of neuroscience research have demonstrated that the lateral PFC is comprised of neurons that are exquisitely sensitive to behaviorally informative associations (for a review, see [51]). This work has focused on the lateral PFC because it represents a site of convergence of the information needed to synthesize multimodal information from a wide range of brain systems. The lateral PFC consists of three major subregions that each emphasize processing of particular information based on their interconnections with specific cortical regions (Figure 1).

Ventrolateral PFC (vlPFC) is heavily interconnected with cortical areas for processing information about visual form and stimulus identity (inferior temporal cortex), supporting the categorization of environmental stimuli in the service of goal-directed behavior. Dorsolateral PFC (dlPFC) is interconnected with cortical areas for processing auditory, visuospatial, and motor information, enabling the regulation and control of responses to environmental stimuli. Finally, anterolateral PFC (alPFC) is indirectly connected (via the ventromedial PFC) with limbic structures that process internal information, such as emotion, memory, and reward [52–55]. The lateral PFC therefore enables the integration and synthesis of information across this broadly distributed network of modal brain regions [7].

Once modality-specific representations within this broadly distributed network are captured by a set of conjunctive neurons in the lateral PFC, the set can later activate the pattern in the absence of bottom-up stimulation, producing a *simulation* of the event sequence [5–10,47, 48]. For example, on entering a familiar situation and recognizing it, a simulation that represents the situation becomes active. Typically the entire situation is not perceived initially. A relevant person, setting, or event may be perceived, which then suggests that a particular situation is about to play out. The simulation can be viewed as a complex configuration of multimodal components that represent the (i) situation (including agents, objects, actions, mental states, and background settings) and (ii) causal and associative relations that hold among its elements [10,56–59]. Because part of this pattern matched the current situation initially, the larger pattern became active in memory. The remaining parts of the pattern – not yet observed in the situation – constitute inferences, namely predictions about what will occur next or explanations for observed behavior [5–7].

To the extent that the simulation is entrenched in memory, pattern completion is likely to occur automatically. As a situation is experienced repeatedly, its simulated components and the associations linking them increase in potency. Thus when one component is perceived initially, these strong associations complete the pattern automatically. We propose that behavior-guiding principles for social inference are mediated by deeply entrenched simulations, whose learned associations are the product of evolutionarily adaptive cognitive and neural mechanisms [34–43].

The observed role of simulation mechanisms for social inference in non-human primates supports this account [60], suggesting that modality-specific simulations represent continuity of social information processing across the species [61]. According to this framework, social interactions initially match modality-specific representations in one or more simulations that

have become entrenched in memory. Once one of these wins the activation process, it provides inferences via pattern completion [62]. Simulations representing necessary (obligatory or prohibited) courses of action motivate expectations concerning specific actions the perceiver and recipient must take, whereas simulations for possible (permissible) forms of behavior represent a broader range of outcomes, motivating expectations about courses of action the perceiver and recipient may take. The unfolding of inferences about necessary and possible states of affairs – realized as a simulation – represent behavior-guiding principles for the orchestration of social thought and action [5–11,47,48]. The recruitment of specific lateral PFC subregions for social inference is determined by the evolution, development, hierarchical structure, and anatomical connectivity of the PFC (Box 1). We now turn to a review of emerging neuroscience evidence investigating the proposed inferential architecture of the lateral PFC.

Inferential architecture of lateral prefrontal cortex

We review a broad range of evidence from the social and decision neuroscience literatures demonstrating (1) the involvement of vIPFC when reasoning about necessary (obligatory or prohibited) courses of action, (2) the recruitment of dlPFC for drawing inferences about possible (permissible) states of affairs, and (3) activation in alPFC for higher-order inferences that incorporate both categories of knowledge (Figure 2). The simulation architecture underlying these forms of inference further predicts the recruitment of broadly distributed neural systems, incorporating medial prefrontal [4–6,9–11] and posterior knowledge networks representing modality-specific components of experience. Our review examines functional neuroimaging (fMRI) data in healthy volunteers, neuropsychological studies of brain-injured patients, and repetitive transcranial magnetic stimulation (rTMS) evidence, identifying the recruitment of distinct and often lateralized subregions of the lateral PFC for alternative forms of human inference.

Ventrolateral prefrontal cortex

An increasing number of fMRI studies have shown that social norms for necessary (obligatory or prohibited) courses of action are represented by vIPFC (areas 44, 45, and 47; Figure 2b). Fiddick and colleagues [12] observed activity within bilateral vIPFC (area 47) for social exchange reasoning, employing stimuli consisting primarily of social norms for obligatory and prohibited courses of action. Converging evidence is provided by Berthoz and colleagues [13], who demonstrated the recruitment of left vIPFC (area 47) when participants detected violations of social norms stories representing obligatory and prohibited courses of action (e.g., the decision to “spit out food made by the host”). Similarly, Rilling and colleagues [14] reported activation within left vIPFC (area 47) when participants detected the violation of obligatory and prohibited norms of social exchange in a Prisoner’s dilemma game (i.e., the failure to cooperate).

The decision neuroscience literature further supports this framework, demonstrating the involvement of vIPFC when drawing conclusions that necessarily follow from the truth of the premises, that is, for *deductive inference*. Although wide consensus in the literature has not yet been reached, an increasing number of studies report consistent findings when common sources of variability are controlled (regarding the linguistic content, linguistic complexity, and deductive complexity of reasoning problems). A recent series of experiments by Monti and colleagues [63] controlled for these sources of variability and provided evidence that left vIPFC (area 47) mediates representations of the logical structure of a deductive argument (e.g., If *P* or *Q*, then *Not-R/P*/ Therefore, *Not-R*), supporting the representation of behavior-guiding principles for necessary forms of behavior within this region. Furthermore, a recent study by Kroger and colleagues [64] controlled for the complexity and type of calculations that were performed and also observed activation within left vIPFC (areas 44 and 45) for deductive reasoning (see also [65]). Additional supporting data are provided by Goel and colleagues

[66,67], who have consistently observed activation within left vIPFC (areas 44 and 45) for deductive conclusions drawn from categorical syllogisms (e.g., All humans are mortal/Some animals are human/Therefore, some animals are mortal). Finally, Noveck and colleagues [68] demonstrated recruitment of left vIPFC (area 47) for drawing deductive conclusions from conditional statements (e.g., If *P* then *Q*/Therefore, *Q*), consistent with the role of this region for representing behavior-guiding principles in the form of a conditional.

Dorsolateral prefrontal cortex

Accumulating evidence demonstrates that dlPFC (areas 46 and 9) represents behavior-guiding principles for evaluating the permissibility or fairness of observed behavior (Figure 2c). An early study by Sanfey and colleagues [69] reported activity within right dlPFC (area 46) when participants evaluated the fairness of an offer in an ultimatum game. Knoch and colleagues [70] further demonstrated that deactivating this region with rTMS reduced participants ability to reject unfair offers in the ultimatum game, suggesting that dlPFC is central for guiding behavior based on evaluations of fairness and permissibility. Additional evidence is provided by Buckholz and colleagues [15], who observed activity within right dlPFC (area 46) when participants assigned responsibility for crimes and made judgments about appropriate (e.g., equitable or fair) forms of punishment in a legal decision making task. Similarly, Spitzer and colleagues [71] demonstrated that social norm compliance recruits a lateral prefrontal network, with right dlPFC (area 46) mediating subjective representations of punishment enforced for violating socially appropriate forms of behavior (for additional discussion, see [72]). The work of Greene and colleagues [16] further suggests that this region is involved in normative evaluations involving conflicting moral goals. These authors employed moral scenarios similar to the famous trolley problem [73] and assessed trials in which participants acted in the interest of greater aggregate welfare at the expense of personal moral standards. This contrast revealed reliable activation within right dlPFC (area 46), suggesting that this region is critical for evaluating the permissibility or fairness of behaviors that conflict with personal moral standards (for additional evidence, see [17, 74]).

Further evidence to support this framework derives from the decision neuroscience literature, which demonstrates the involvement of dlPFC when drawing conclusions about possible or permissible states of affairs. In contrast to deductive inference, conclusions about possible courses of action reflect uncertainty concerning the actions that *should* be taken and/or the consequences that *might* follow, and are referred to as *inductive inferences*. Volz and colleagues [75] found that activation within right dlPFC (area 9) increased parametrically with the degree of uncertainty held by the participant (see also, [76]). Furthermore, Osherson and colleagues [77] observed preferential recruitment of right dlPFC (area 46) when performance on an inductive reasoning task was directly compared to a matched deductive inference task, supporting the role of this region for reasoning about possible (rather than necessary) states of affairs.

Anterolateral prefrontal cortex

A large body of neuroscience evidence demonstrates that alPFC (areas 10 and 11) – and the orbitofrontal cortex (OFC) more broadly – is central for social cognition (Figure 2d). Studies of patients with lesions confined to OFC have reported impairments in a wide range of social functions, including the regulation and control of social responses, the perception and integration of social cues, and perspective taking [20–23]. Recent evidence from Stone and colleagues [39] further demonstrates that patients with orbitofrontal damage produced selective impairments in reasoning about social contracts, supporting the proposed role of the PFC in goal-directed social behavior. Bechara and colleagues [21] observed profound deficits in the ability of OFC patients to represent and integrate social and emotional knowledge in the service of decision making. Converging evidence is provided by LoPresti and colleagues [22], who

demonstrated that left aPFC (area 11) mediates the integration of multiple social cues (i.e., emotional expression and personal identity), further suggesting that this region supports the integration of multiple classes of social knowledge.

Additional support derives from the decision neuroscience literature, which demonstrates that progressively anterior subregions of the lateral PFC (areas 10 and 11) are associated with higher-order processing requirements for thought and action [78–80]. Ramnani and Owen [81] reviewed contemporary research and theory investigating the cognitive functions of aPFC, concluding that this region is central for integrating the outcomes of multiple cognitive operations, consistent with the predicted role of aPFC for representing higher-order inferences that incorporate both necessary and possible states of affairs (for representative findings, see [64,82–85]).

Toward an integrative theory of human inference, value, and belief

We have reviewed converging lines of evidence to support an evolutionarily adaptive neural architecture for social reasoning within the lateral PFC, drawing upon recent theoretical developments in evolutionary psychology and neuroscience studies investigating the biology, evolution, ontogeny, and cognitive functions of this region. We have surveyed a broad range of social and decision neuroscience data demonstrating that the lateral PFC mediates behavior-guiding principles for specific classes of inference, with vLPFC recruited when drawing inferences about necessary (obligatory or prohibited) courses of action, engagement of dLPFC when reasoning about possible (permissible) behavior, and aPFC recruited when both categories of inference are utilized (Figure 2). These findings set the stage for new approaches to understanding human thought – in terms of its evolutionarily adaptive functional organization and the constraints it places on the formation of human systems of value and belief – from the level of genes and neurons to thought and behavior.

Nature provides a seemingly unbounded variety of complex functional structures, from mechanisms for social behavior in insects to the neural architecture that enables social reasoning in humans. Until recently, variation was believed to emerge from random processes, with adaptations shaped solely by natural selection. New molecular approaches have sharpened our understanding of the sources of variation and how developmental programs constrain evolutionary processes, yielding a restricted range of possible adaptations [86]. Our review elucidates the neural architecture that has emerged from these processes to support social reasoning, identifying functionally organized machinery that is too improbably well ordered to have arisen by chance (Figure 2).

An evolutionarily adaptive neural architecture for human inference raises new possibilities for understanding questions of evolution and human intelligence (see Outstanding Questions Box), suggesting that research and theory from anthropology, evolutionary psychology, social psychology, political science, behavioral economics, and decision neuroscience can be productively combined to understand one of the most profound problems of intellectual life: how humans evolved the capacity to represent and reason about necessity and possibility, and to productively apply this knowledge to construct systems of moral [87–89], ethical, legal, and political belief. By investigating the evolutionary origins of this knowledge – assessing the formation of normative principles for social behavior and their extraordinary range of cultural expression – the burgeoning field of social cognitive neuroscience will continue to advance our understanding of the remarkable cognitive and neural architecture from which uniquely human systems of value and belief emerge.

Box 1**An Evolutionarily Adaptive Neural Architecture for Social Reasoning**

The functional organization of the lateral PFC is determined by the evolution, development, hierarchical structure, and anatomical connectivity of the PFC.

Evolution and development

Research investigating the evolution and ontogeny of the PFC demonstrates that the lateral PFC initially emerged from ventrolateral prefrontal regions, followed by dorsolateral, and then anterolateral cortices [54,90]. From an evolutionary perspective, the emergence of lateral PFC subregions reflects their relative priority for the formation of organized social groups, with vlPFC signaling the onset of social norms for necessary (obligatory or prohibited) courses of action, providing the foundations for standards of conduct that are central for the organization of society. Social norms for permissible behavior later enabled the representation of a broader range of possible outcomes, supporting the assessment of alternative forms of goal-directed behavior within dlPFC. Finally, the evolution of alPFC enabled processing of higher-order relations and reasoning about complex forms of social behavior involving necessary and possible courses of action. Consistent with its evolutionary development, the ontogeny of the lateral PFC reflects the importance of first representing social norms for necessary behavior (i.e., fundamental rules the child must obey), followed by an understanding of permissible courses of action (e.g., guided by judgments of equity and fairness), and finally high-order inferences involving both forms of representation [91].

Hierarchical organization

An emerging body of evidence further demonstrates that the anterior-to-posterior axis of the lateral PFC is organized hierarchically, whereby progressively anterior subregions are associated with higher-order processing requirements for planning and the selection of action (for recent reviews, see [78–81]). Thus, processes within the lateral PFC respect the hierarchical organization of this region, with progressively anterior regions representing simulations that support higher-order inferences incorporating both necessary and possible states of affairs.

Anatomical connectivity

The connectivity of lateral PFC subregions embodies an evolutionarily adaptive neural network for goal-directed social behavior. From an evolutionary perspective, behavior requested by members of high social status represents necessary courses of action that a lower ranking individual must follow. This provides one explanation for why neural systems for identifying the social status of individuals (based on representations of visual form and stimulus identity) are anatomically connected with ventrolateral prefrontal regions for drawing inferences about necessary courses of action. An intriguing study by Marsh and colleagues [92] supports this proposal, demonstrating that vlPFC (area 47) is selectively recruited when processing status poses for individuals of high (rather than low) social status – providing a unified neural architecture for identifying individuals of high social status and the necessity of obeying their commands. An evolutionary perspective further suggests that social norms for possible (permissible) behavior are central for achieving adaptive goals within society [34–43], providing one explanation for why dorsolateral prefrontal regions for drawing this type of inference are anatomically connected with brain regions for the regulation and control of behavior. Finally, adaptive behavior guided by both categories of inference draws upon higher-order representations that incorporate multiple forms of social

inference and therefore recruits aPFC regions that enable representations of greater complexity (e.g., incorporating emotion and memory).

Box 2

Outstanding Questions

- What role does the lateral PFC play in the formation of human belief systems? In what manner does the neural and computational architecture of this region constrain the form and expression of moral [87–89], ethical, and political beliefs? How do these constraints in turn shape the formation of society and invariant properties of human culture?
- What cognitive operations are implemented within the lateral PFC to support human inference? Does this region (i) serve as an integrative hub for the synthesis of modality-specific representations [93], (ii) contain mechanisms that control the selection and processing of modality-specific knowledge [51], or (iii) incorporate both representational and processing functions [5–10,47,48].
- In what sense and to what degree does the inferential architecture of the lateral PFC represent intuitive, affective, and deliberative processes? How do these decision components together contribute to human reasoning?
- How are inferences concerning necessary and possible states of the world represented within dual process theories that distinguish between the neural and computational architecture of intuitive versus deliberative processes [1,57]?
- The involvement of the lateral PFC for processing social and non-social knowledge raises the question of whether behavior-guiding principles for social inference are mediated by domain-specific (rather than domain-general) neural systems (for recent neuroscience reviews, see [9,10]).
- What evolutionary and biological principles account for the observed lateralization of inferences concerning necessary (left hemispheric) versus possible (right hemispheric) courses of action (Figure 2)?
- The reviewed evidence derives primarily from functional neuroimaging studies (fMRI) that establish an association between specific lateral PFC subregions and forms of reasoning. The necessity of this region and its precise contribution to the neural systems mediating human inference, however, remains controversial [94], raising the question of how the involvement of lateral PFC should be characterized: Is this region associated with and/or necessary for the reviewed categories of inference?
- Evolutionary psychologists have identified a broad range of evolutionarily adaptive cognitive heuristics that support decision making (for a review, see [95]), motivating further research and theory investigating how cognitive heuristics are implemented within the neural and computational architecture of the lateral PFC.
- The evolutionary origins and biological bases of behavior-guiding principles for human inference motivate the question of whether normative standards for human rationality should be constructed from formal mathematical and logical systems, or instead assessed in terms of the evolutionary conditions and ecological contexts that have shaped the inferential architecture of the human mind [34–43].

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Dorsolateral PFC

Auditory, visuospatial, and motor information

Anterolateral PFC

Emotion and memory

Ventrolateral PFC

Visual form and stimulus identity

Figure 1. Integrative anatomy of the macaque monkey prefrontal cortex (PFC). Numbers refer to subregions within the lateral PFC defined by Brodmann. Modified with permission from Reference [51].

Figure 2a

Figure 2b

Figure 2c

Drawing inferences about possible states of affairs

Figure 2d

Drawing inferences about higher-order relations

Figure 2.

An evolutionarily adaptive neural architecture for social reasoning. (a) The functional organization of the lateral prefrontal cortex (PFC) which is symmetric in both hemispheres is summarized (b), (c) and (d) illustrate supportive evidence. Panels (b) and (d) illustrate the left hemisphere, and panel (c) depicts the right hemisphere.

Figure Box 1.

Ontogenetic map of the prefrontal cortex (PFC) according to Flechsig [90]. The numeration of the areas indicates the order of their myelination. Modified with permission from Reference [90].