

## Review

An Integrative Interdisciplinary  
Perspective on Social  
Dominance Hierarchies

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**In the course of evolution, social dominance has been a strong force shaping the organization of social systems in many species. Individuals with a better ability to represent social dominance relationships and to adapt their behavior accordingly usually achieve better access to resources, hence providing benefits in terms of reproduction, health, and wellbeing. Understanding how and to what extent our brains are affected by social dominance requires interdisciplinary efforts. Here, we integrate findings from social neuroscience, evolutionary biology, and developmental psychology to highlight how social hierarchies are learned and represented in primates. We also review neuropharmacological findings showing how dopamine, serotonin, and testosterone influence social hierarchies and we emphasize their key clinical implications on vulnerabilities to neuropsychiatric disorders.**

## Perspectives on Dominance Hierarchies

**Social hierarchies** (see [Glossary](#)) characterize the group structure of many species. Because **dominance hierarchies** often mean individuals within the group have asymmetric access to resources, including food and reproductive partners, they are a major evolutionary force [1,2]. Not only are there benefits to obtaining a dominant position within the hierarchy, but the accurate representation of dominance relationships can help individuals form effective social alliances.

Although social hierarchies play a central role in shaping and transforming interindividual relationships across social groups over time, social dominance has most often been studied as an explicit static variable rather than as an implicit dynamic variable constantly modified by social events. The cognitive processes underlying emergence of social hierarchies have been investigated through separate approaches in the fields of developmental psychology, social neuroscience, genomics, evolutionary biology, and neuropharmacology. In order to address the fundamental questions that encompass these domains, neurocomputational approaches highlighting the mechanisms at play when learning social dominance relationships might be key. A better consideration of egocentric versus allocentric learning mechanisms may also help reconciling different lines of research in healthy and in clinical populations (see reference frame section). Moreover, because it occurs in multiple time-scales and shapes specific neural circuits, social dominance learning is particularly important to understand the evolution of dominance representations and their associated behaviors from childhood to adulthood.

## Trends

The drive to occupy a specific social dominance status is deeply rooted in the biology and evolutionary history of our species.

Dominance hierarchies emerge early in development, and children use a variety of cues to learn about social dominance relationships.

Learning social hierarchy information engages the anterior mPFC, both when learning ranks by observation and when learning by direct dyadic competitive interactions.

The neurocomputational mechanisms at play when learning social hierarchies have been identified using model-based fMRI.

Dopamine, serotonin, and testosterone are central to the emergence of social hierarchies across species.

Understanding the neural bases of social dominance hierarchies is key to explain interindividual differences in human cognition and has important clinical implications.

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The goal of this review is to offer a balanced account of these approaches to provide a neurobiological foundation of how primates represent, learn, and navigate social dominance relationships. Understanding how specific brain circuits work, develop, and are modified by social environment may help us to identify dysfunctional mechanisms in neuropsychiatric disorders and a large array of somatic diseases (e.g., hypertension) for which psychosocial stress plays a pivotal role [3–5]. We first present recent advances revealing three human brain networks engaged in representing social dominance from cues, when learning social ranks by observation and through direct competition. Then, we describe parallels between the brain systems engaged when learning social ranks and those observed in the field of social learning in self (egocentric) versus other (allocentric) **frames of reference**. Next, we review progress revealing the neuroanatomy of social dominance in non-human and human primates. In light of the three processes introduced above (representing dominance relationships from cues, learning by observation and through direct competition), we then discuss recent developmental studies showing how children represent social hierarchies. Because growing evidence from animal research suggests that dopamine and serotonin (5-hydroxytryptamine) are not only crucial for associative learning but also for social learning, we discuss the influences of these neuromodulators and of testosterone on social dominance behavior. Finally, because maladaptive appraisal of social dominance constitutes a significant source of vulnerability for neuropsychiatric disorders characterized by impaired social cognition, such as depression, social anxiety, and autism, we present clinical implications of these neuropharmacological findings [3–6].

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## Neurobiology of Social Dominance Representation in Primates

Social dominance is deeply rooted in the biology and evolutionary history of our brains (Box 1) and most social species can assess it in several ways. First, animals can rely on dominance cues (e.g., body size, aggressive facial expressions, and physical attributes) to rapidly assess the strength of potential competitors and to avoid costly physical conflict [7]. Second, animals can learn about dominance hierarchies through **observational learning**. That is, by monitoring the social interactions of other individuals within the group, they can infer dominance relationships. Third, animals can learn about dominance relationships directly through competitive **dyadic interactions** against rivals (experiencing successive victories or defeats

### Box 1. Evolutionary Bases of Social Hierarchies

Recent approaches combining models from evolutionary game theories and evolutionary anthropology describe how **leadership** evolved as strategies to coordinate group activities [98]. This growing area of research in theoretical biology and social sciences explains the emergence and maintenance of leadership. The emergence of leadership is paradoxical according to theories because fully shared decisions should emerge if time is not a crucial factor [99]. However, due to inefficient collective decisions to reach a consensus within a group, leaders do emerge. Many factors can influence theoretical models of the emergence of leadership, such as partial information between group members, differential power or resource control, personality variation, imitation of leaders by other group members [100], and costly punishment by leaders [101–104]. These models indicate that hierarchies tend to be more attenuated when (i) resources are more difficult to monopolize; (ii) sharing resources is essential for survival; (iii) individuals can easily leave groups; and (iv) individuals form coalitions to overthrow a dominant. Overall, models of leadership demonstrate that leaders and followers can emerge naturally as a result of heterogeneity in these factors, and that leadership tends to be beneficial to both social groups and individual members of these groups [98].

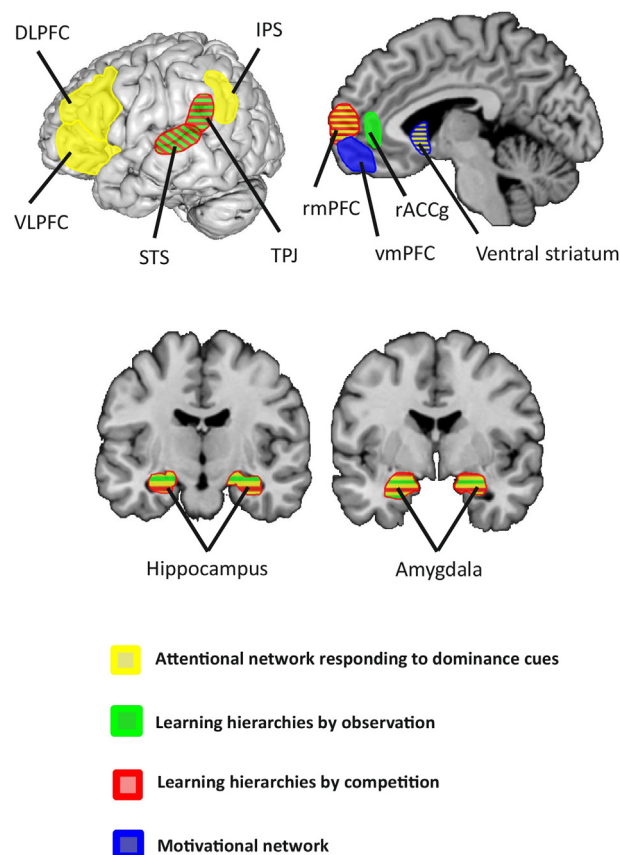
Another approach investigating the expression and transmission of social dominance comes from behavioral genetics and genetic association studies [105]. Although high dominance rank covaries with reproductive success and food access [106], thereby conferring a clear selection advantage, whether or not social dominance can be inherited within a population is still controversial [105]. Selective breeding for social dominance is possible in the laboratory [107,108] and dominance can be inherited in specific species in the wild [109,110], but no gene that exclusively promotes social dominance has so far been identified. Rather, it has been argued that indirect genetic effects act via behavioral dimensions such as personality differences in trait anxiety, susceptibility to stress, agonistic tendencies, motivational processes, and sociality derived from affiliative (grooming and spatial proximity) interactions [105]. Genes that have received particular interest regarding social hierarchies are known to modulate related traits, such as motivation, reward processing, and aggression.

against competitors). Each of these processes can be engaged at different stages depending on how dominance interactions are experienced in the environment.

The brain circuits engaged in the representation of social dominance relationships encompass three partially overlapping brain networks, which reflect the typology of the processes described above (Figure 1). Below, we detail the evidence of these divisions, coming from functional and structural neuroimaging studies in humans and non-human primates.

### Neural Representation of Hierarchies Based on Dominance-Related Cues

Over the past decade, social neuroscience has identified a large network of brain regions engaged in social decision-making [8,9]. Early neuroimaging studies have investigated the human neural representation of social hierarchies using the perception of social ranks based on



#### Trends in Cognitive Sciences

**Figure 1. Main Brain Networks Engaged in Human Neuroimaging Studies.** Networks when representing social hierarchies based on the perception of social ranks from visual cues (yellow); when learning social hierarchies by observation (green); and by direct dyadic competition (red). The classical motivational network is also represented in blue. These brain networks are composed of: (i) an attentional network responding to dominance cues, including the bilateral prefronto-parietal cortices (yellow); (ii) a network engaged in learning hierarchies by observation composed of the TPJ, STS, and rACCg (green); and (iii) a network reflecting learning hierarchies by competition recruiting the rmPFC (BA 10), extending to the dorsomedial prefrontal cortex (red). The fourth motivational network (blue), composed of the vmPFC and the ventral striatum, is engaged in learning from one's actions and rewarded outcomes. Areas engaged in overlapping processes are the ventral striatum, TPJ, STS, amygdala, and hippocampus (hatched lines). Abbreviations: DLPFC, dorsolateral prefrontal cortex; IPS, intraparietal sulcus region; rACCg, rostral anterior cingulate gyrus; rmPFC, rostromedial prefrontal cortex (BA 10); STS, superior temporal sulcus region; TPJ, temporo-parietal junction; VLPFC, ventrolateral prefrontal cortex; vmPFC, ventromedial prefrontal cortex.

### Glossary

**Aggression:** behavior with the intent of inflicting physical or psychological harm on another individual.

**Bayesian inference scheme:** method of statistical inference in which Bayes' theorem is used to update the probability for a hypothesis as more evidence or information becomes available.

**Dominance:** tendency to prevail when one's goals conflict with those of another agent.

**Dominance hierarchy:** organization of individuals in a group into those that are dominant and those that are submissive, as part of a competition for resources. In dominance hierarchies, individuals achieve priority access to resources through threat, intimidation and displays of force.

**Dyadic interactions:** social interactions between two individuals. Competitive dyadic interactions lead to successive experience of victories or defeats against competitors during fights with another individual.

**Frames of references:** refers to a specific agent (e.g., self or other) involved during social interactions.

**Leadership:** refers to a special position in the decision-making hierarchy where individuals exercise disproportionate influence on group decision-making, and can gain priority access to resources in return.

**Model-based functional magnetic resonance imaging (fMRI):** method used for investigating the computational role of different brain regions. Computational models of behavior are first used to shed light on latent variables of the models and then to find the brain regions covarying with variables of the models.

**Observational learning:** allows an agent to learn about the value of stimuli or actions not through direct experience but instead through observing the behavior of another agent.

**Power:** ability to influence others by exerting control over others' behavior, resources, or outcomes.

**Prediction error:** signal reflecting the difference between predicted and delivered outcomes.

**Reactive aggression:** defensive response to perceived or actual provocation. It involves retaliation and is characterized by anger and often accompanied by disinhibition,

visual cues, such as explicit representation of ranks [10], postures [11,12], uniforms [13], facial traits [14], as well as intelligence, celebrity, or height [15,16]. These studies have revealed an attentional network, including the lateral prefrontal cortex (PFC) and the intraparietal sulcus region, responding to dominance cues and engaged in rank perception in a broad set of tasks (Figure 1, yellow). Some of these studies also recruit areas, such as the rostromedial PFC (rmPFC), the amygdala, the hippocampus, the ventral striatum, and the fusiform gyrus, showing overlapping activations engaged with other processes, such as the motivation to win or to avoid losing and the affective experience accompanying victories and defeats (hatched lines, Figure 1).

Yet, one limitation of these studies (reviewed in [7,17]) is that many of these regions may be related to general attentional, emotional, and inferential processes associated with hierarchy processing rather than to the neural representation of hierarchy *per se* [18]. For example, dominance features from computer-generated faces recruit part of the network mentioned above more robustly in those participants showing stronger avoidance behavior in response to facial dominance traits [19]. In an attempt to circumvent these limitations, a recent study used faces previously encountered in competitive interactions to show that the dorsolateral PFC (DLPFC) and superior temporal sulcus (STS) discriminate dominant from subordinate individuals in passive viewing contexts [20]. Moreover, the engagement of the DLPFC in response to dominant individuals was more pronounced in people valuing more the existence of dominance hierarchies.

In non-human primates, with which we share common evolutionary ancestry, viewing videos of social interactions selectively engaged a brain network sharing areas with both the attentional and observational learning networks reported in humans, including the rostral part of the anterior cingulate gyrus (rACCg), the ventrolateral PFC (VLPFC), the STS, and a temporoparietal cluster (Figure 1) [21]. This indicates a close link between the networks engaged in attention to dominance cues, observational learning (see below), and observing social interactions in both non-human and human primates.

When decisions are made in a social context, a critical problem faced by the brain is the need to learn from interactions with conspecifics and to subsequently behave adaptively, while taking into account the intentions of others. Although the neural mechanisms underlying strategic reasoning during social interactions has begun to be identified [22], little is known about the neurocomputational processes which underlie learning of social dominance relationships (Box 2). Moreover, it is still unclear as to whether activity in any of the aforementioned regions is causally involved in dominance-related behaviors. These mechanisms and their neural implementations can be identified using **model-based functional magnetic resonance imaging (fMRI)** and mathematical learning models widely used for learning stimuli-outcomes relationships in nonsocial settings (Box 2). Hereafter, we review model-based fMRI studies that recently investigated how the human brain learns social dominance relationships, either by observation or through competitive dyadic interactions [23–25].

### Neural Representations of Hierarchies Learnt by Observation

Monitoring social interactions by observation of other individuals allows animals to infer dominance relationships, favoring competition against likely future losers and seeking alliances with those who are likely to win. In a recent model-based fMRI study in humans, participants learned ranks through the observation of pairwise contests [24]. Participants had to select between which of two faces they thought had more **power** while receiving corrective feedback (Figure 2A). Participants acquired and represented transitive ranking relationships. The medial PFC (mPFC), and more specifically the ACCg, was engaged in learning ranks, computing estimates of individuals' power within a hierarchy, and updating knowledge about one's own hierarchy [24]. The neurocomputational processes at play were better accounted for by a

affective instability, and high levels of arousal.

**Reinforcement learning:** area of machine learning concerned with how agents take actions in an environment to maximize cumulative rewards.

**RL-ELO:** Reinforcement learning algorithm based on the Elo rating system, which is a method for calculating the relative skill levels of players in competitor-versus-competitor games such as chess. It is named after its creator Arpad Elo.

**Social hierarchy:** coherent and generally agreed upon ranking of a group of individuals along one or more social dimensions bearing relevance to that group.

**Social status:** relative rank of an individual along one or more social dimensions within a given social hierarchy.

**Transitive inferences:** form of deductive reasoning that allows one to derive a relation between items that have not been explicitly compared before (i.e., ability to deduce that if A is related to B and B is related to C, then A must be related C).

**Box 2. Neurocomputational Mechanisms at Play for Learning Ranks**

The neurocomputational processes that underlie the learning of social dominance status have been identified using both reinforcement learning (RL) and **Bayesian approaches** [24,25]. Social learning can be accounted for by RL mechanisms in a wide range of tasks [24,111–115]. In this regard, social learning, and learning about social hierarchies, is not so different to RL used to learn stimuli–outcomes relationships [22,116]. Yet, when decisions are made in a social context, the degree of uncertainty about the possible outcomes increases dramatically because the behavior of other group members can be much more difficult to predict than the physics of the environment. This makes it challenging to study the nature of the computational algorithms that can account for primate social decision making.

One powerful theoretical approach to studying social decision-making has been to hypothesize that the brain performs Bayesian inferences based on observations using probabilistic representations of the world and utilizes the results of Bayesian inferences to choose optimal actions. Such Bayesian approaches are better able to capture participants' data in social hierarchy learning [24] and in inferring another agent's intentions – from observing actions in partially observable domains – [117,118] than improved RL models (such as RL-ELO models [24]). In such models, subjects treat the powers of individuals as a hidden variable, about which they make approximate Bayesian inferences based on the likelihood of observations. Related models such as the Microsoft TrueSkill algorithms are widely used in the online gaming industry, where winning and ranking are key motivational drives, to rank high number of human players in an efficient way.

The Bayesian and RL frameworks differ in fundamental aspects, including the capacity for Bayesian models to learn large hierarchies and to represent uncertainty in the estimation of power. The models also differ in the nature of the mechanism by which they update their estimates of the power of individuals within the hierarchy [24]; RL models usually only update the values of the current items in a trial, while Bayesian models usually update the values of all items at once (e.g., the posterior distribution of a rank system). Yet, when the outcome of competitive contests depends on a complex array of variables including self- and other-performances, when dominance relationships have no reason to follow a strictly transitive ranking system and when affective factors bias social learning, RL algorithms might be more ecologically relevant and computationally tractable than Bayesian schemes.

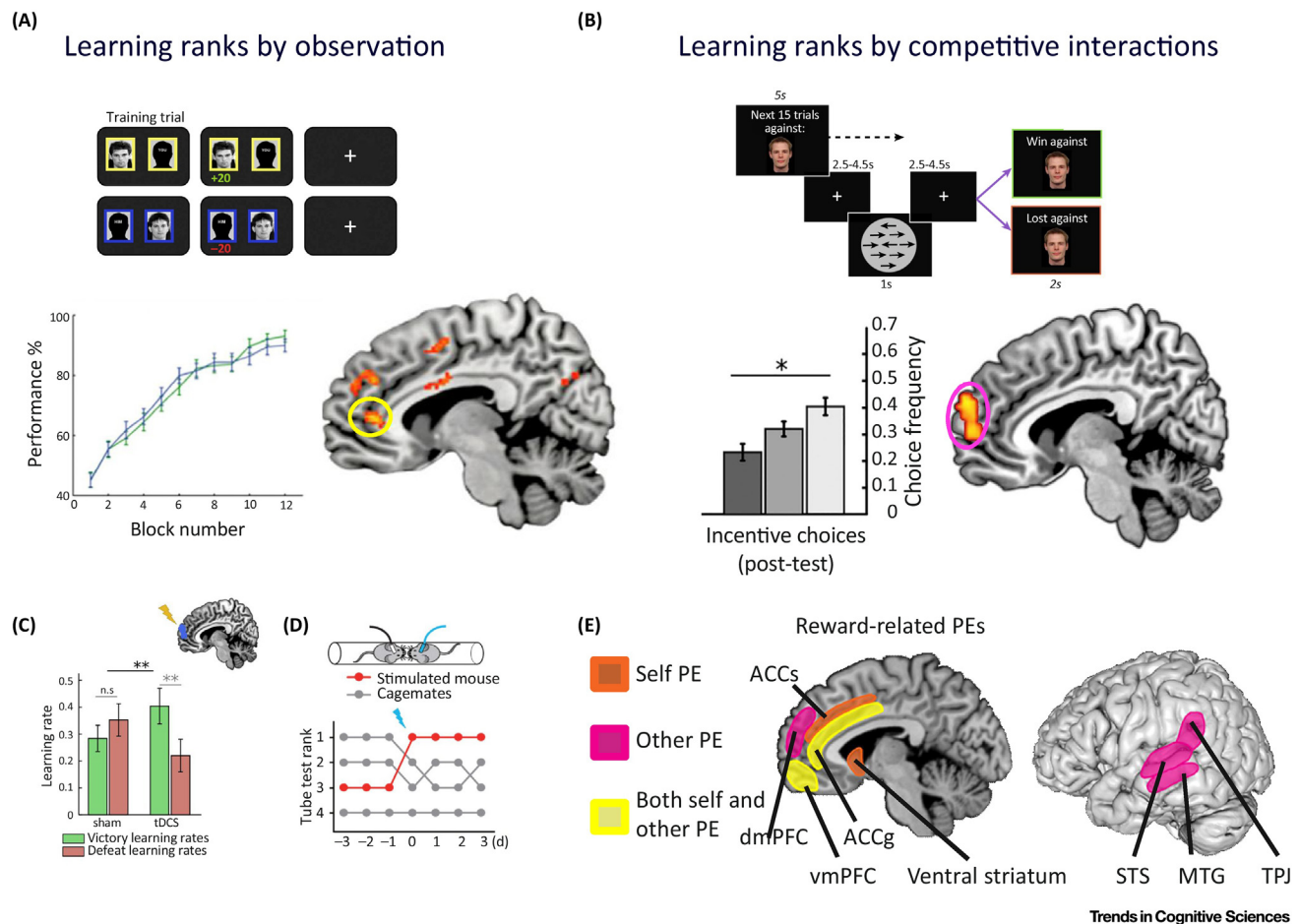
**Bayesian inference scheme**, which tracked the power of individuals than by a **reinforcement learning** model inspired from the chess rating system (RL-ELO) (Box 2). Thus, learning ranks through transitive inference and trial-and-error while observing pairwise contests without participating to the contest oneself, may rely on similar computational mechanisms as previously identified in one particular form of observational learning [9], which consists in the updating of hidden mental state representations during strategic interactions [26–30].

Neural activity in the amygdala and anterior hippocampus has also been shown to track the emergence of knowledge about social hierarchies, with the hippocampus being also involved in the representation of nonsocial hierarchies [31]. Yet, the precise role of these regions remains controversial, because they have been reported with all processes described above and their encoding of social ranks appears to be context-dependent [7,17,24,25,31,32] (Figure 1). Interestingly, a recent study showed that the same hippocampal mechanisms that support spatial navigation may be engaged in the computation of social spaces according to two factors that define social relationships: dominance and affiliation computed in an egocentric reference frame (see section on reference frames) [33]. How the neural computations engaged for coding social space/social network and spatial maps relate to each other will be an important question to investigate for future research [33–36].

**Neural Representation of Hierarchies Learnt through Direct Competitions**

Learning dominance ranks through direct contests with others can be costly in terms of time, energy, and potential physical damage. Yet, such learning processes ultimately guide the establishment of social dominance hierarchies in many species and are crucial when deciding to engage in cooperative or competitive interactions with others [10,23,37]. Using a competitive task mimicking ecological situations where social dominance is acquired through direct competition with others, resulting into avoidance of stronger opponents, a recent human model-based fMRI study investigated learning of social hierarchies [25] (Figure 2B). The results

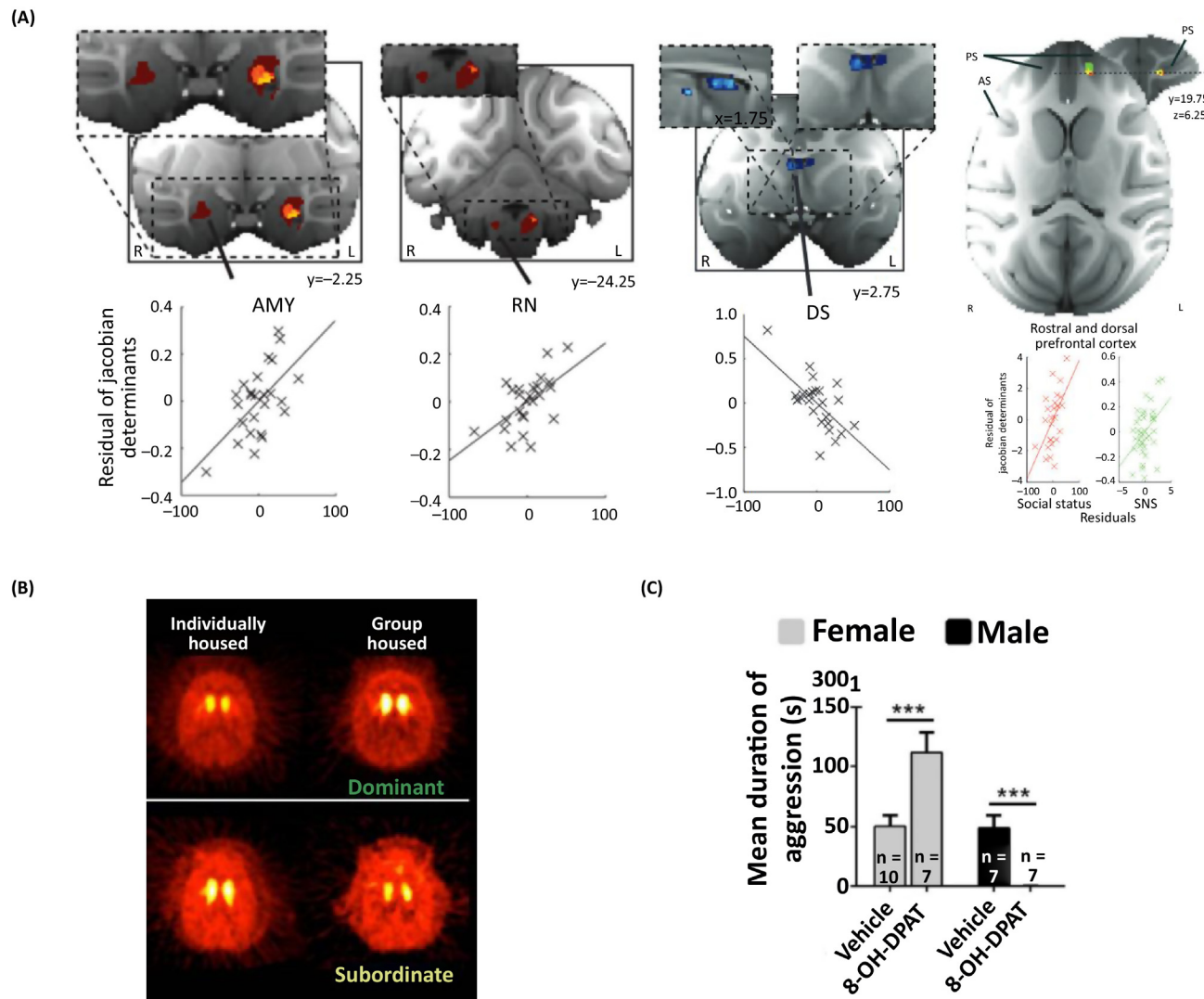




**Figure 2. Engagement of Specific mPFC Regions in Learning Ranks by Observation or by Competitive Interactions.** (A) Top. Learning ranks by observation tested with model-based fMRI using a task requiring one to select who has more power between two people followed by corrective feedback. Bottom. Behavioral results showing that participants learned the hierarchies by trial and error (self condition: green; other condition: blue). Right. Significantly greater correlation occurred between rACCg activity and updating of hierarchy knowledge in self versus other condition. Adapted, with permission, from [24]. (B) Top. Learning ranks by dyadic competitive interactions, such as contests in nature, has been assessed with model-based fMRI using a competitive game in which participants were led to believe that they were playing against opponents in real time. Bottom. Participants learned the rank of the opponent after winning or losing in the competitive task (dark grey: superior individual, light grey: inferior individual). Activity in the rmPFC correlated with competitive PE, a teaching signal necessary to learn dominance representations from social defeats and victories in the absence of monetary incentives. Adapted, with permission, from [25]. (C) Causal involvement of the rmPFC in learning and monitoring social dominance. Enhancing rmPFC neural excitability with anodal tDCS in humans modulated the learning parameters that governed the update of dominance representations and enhanced the influence of participants' dominance on competitive choices [25]. (D) Optogenetic activation of the dmPFC in mice induces instantaneous winning in the tube test. Adapted, with permission, from [39]. (E) Brain regions responding to self-referenced reward PE (orange), other-referenced reward prediction errors (pink), or both (yellow). Adapted, with permission, from [41]. Abbreviations: ACCg, anterior cingulate gyrus; dmPFC, dorsomedial prefrontal cortex; fMRI, functional magnetic resonance imaging; MTG, medio temporal gyrus; PE, prediction error; rACCg, rostral anterior cingulate gyrus; rmPFC, rostromedial prefrontal cortex; STS, superior temporal sulcus; tDCS, transcranial direct current stimulation; TPJ, temporo-parietal junction.

showed that neural activity in the rmPFC tracked and updated the dominance status of opponents. This brain region was the only region to encode a signed **prediction error (PE)** for defeats/victories against opponents currently predicted to be inferior/superior. In addition, the amygdala, together with the striatum, were selectively deactivated in response to social defeats while the ventromedial PFC (vmPFC) was the only region activated selectively in response to victories. Thus, a motivational network including the ventral striatum and vmPFC, may underlie the affective meaning of competitive outcomes and tune behavioral parameters relevant to social dominance relationships, such as inhibition or avoidance (Figure 1). Interestingly, defeat-related deactivations in the striatum correlated positively with a measure reflecting more subordinate personality profiles; a finding consistent with previous results showing that

striatal responses to **social status** cues depend on subjective socioeconomic status [38]. Thus, the experience of social subordination may have long time-scale consequences on shaping responses of the motivational network (Figures 1 and 3A and the Neuroanatomical Indicators of Social Dominance section).



**Figure 3. Neuroanatomical, Dopaminergic, and Serotonergic Effects on Social Status/Dominance.** (A) Left. Relationships between GM, social dominance status, and SNS in captive macaques. DBM results where GM is related to increased social status include the AMY and the RN for the positive correlation (red) and the striatum for the negative correlation (blue). Right. Regions of GM significantly correlated with social network size (green) and dominance status (red) were found in the rostral and dorsal PFC in the principal sulcus and in the medial superior temporal sulcus and extending adjacent inferior temporal gyrus. Voxels in which portions of the variance in GM were explained by both social network size and social status are in yellow. Adapted, with permission, from [52]. (B) Measures of dopamine D2/D3 receptor availability increase in dominant female monkeys. Positron emission tomography images (percent injected dose per ml) of a D2/D3 receptor radioligand binding in the caudate nucleus and putamen of a dominant and a subordinate monkey, while individually housed and socially housed. Adapted, with permission, from [84]. (C). Hypothalamic injection of a serotonin 1A agonist (8-OH-DPAT) had opposite effects according to sex, stimulating aggression in female hamsters and inhibiting aggression in males. Adapted, with permission, from [96]. Abbreviations: 8-OH-DPAT, 8-hydroxy-2-(di-n-propylamino)tetralin; AMY, amygdala; AS, arcuate sulcus; DBM, deformation-based morphometric; DS, dorsal striatum; GM, gray matter; PFS, prefrontal cortex; PS, principal sulcus; RN, raphe nucleus; SNS, social network size.

Furthermore, neural computations in the rmPFC, as captured by a classical reinforcement-learning algorithm (Box 2), causally contributed to the emergence of social dominance relationships. This was shown by a further anodal transcranial direct current stimulation (tDCS) experiment performed in an anonymous social setting during a competitive task, in which participants had to decide between who of two individuals to compete against [25]. Enhancing cortical excitability of the same anterior mPFC with tDCS affected two key aspects of social dominance learning: it enhanced the impact of victories relative to defeats (Figure 2C), and increased the overall influence of social dominance on subsequent competitive choices. Interestingly, a recent optogenetic study in mice showed that dorsomedial PFC (dmPFC) activation boosted dominance by initiating and maintaining more effortful behaviors in social competition [39] (Figure 2D). Although homologies between rmPFC in humans and dmPFC in mice cannot be made, these findings converge to suggest a causal role of the mPFC in the establishment of dominance hierarchies across species. Having identified specific mPFC subregions engaged in learning social ranks by observation and through direct competition, it is also important to consider in which reference frames social dominance representations are learnt (see below).

### Learning Social Ranks in Egocentric/Allocentric Reference Frames

Learning social dominance relationships requires to represent the abilities of others relative to one's own, which can be done either by putting oneself in 'other shoes' (allocentric frame) and/or by relying on self-referential mechanisms (egocentric frame). The distinction between learning in self versus other frames of reference has proven fruitful in the field of social learning [40,41], as several studies have investigated the brain systems engaged in learning from self-referenced or other-referenced reward PE (Figure 2E). In the mPFC, authors have reported functional gradients favoring one frame of reference over the other along the rostral/caudal axis or the dorsal/ventral axis [22–24,42–44]. For example, the ACCg, which contains areas 24a/b and 32 in both humans and macaques, signals information in an allocentric frame of reference, responding to the consequences of the actions of others and to the outcomes of one's own decisions (egocentric frame) [40,42,45–47]. By contrast, more dorsal and rostral regions of the mPFC, including the ACCs (areas 24c and 32'), may signal information and PE in an egocentric frame only [22,42]. Likewise, the ventral mPFC is more engaged for self-related judgments while the dmPFC is more engaged when making judgments about others [43,44].

The mPFC regions identified in learning dominance relationships (Figure 2A,B) overlap those engaged in social learning through reward-related PE in different frames of reference (Figure 2E), probably because learning social dominance relationships concerns both the self and others. Indeed, the history of victories and defeats constitute appetitive and aversive social outcomes that can be used to update representations about self-confidence, but they are also informative to update estimates of the skills and dominance status of others. For example, the ACCg was engaged in the learning and representation of social rank information about other individuals when they were part of one's own group (egocentric frame) rather than another group, and this finding remained when focusing only on trials that did not directly involve oneself [24]. Yet, the results of some studies do not convincingly fall in one of the two proposed self-other dichotomies [23]. For example, in a recent study, the ACCg selectively tracked a representation of self-performance rather than other abilities in competitive contexts, whereas the more rostral and dorsal area 9 m encoded both self- and other-performance [23]. Moreover, the encoding of defeat- but not victory-related PE in the ACCg (Figure 2B) suggests a potential interaction of affective processes and frames of references [25]. Thus, further work is needed to better characterize the respective contribution of separate mPFC areas in learning dominance relationships in different reference frames (Figure 2E).



### Neuroanatomical Indicators of Social Dominance

In humans, evidence for a link between neuroanatomy and social dominance remain limited, but a larger amygdala has been associated with better transitivity performance in learning social as opposed to nonsocial hierarchies [35]. Such a link has also been proposed based on correlations with socioeconomic status (SES). For example, children raised in poorer or less-educated families have reduced gray matter volumes in the hippocampus [48,49]. Although the exact mapping between SES and dominance is unclear as dominance hierarchies emerge within every social class [50], investigating the link between hippocampal development and the appraisal of dominance relationships may help to understand the susceptibility to antisocial social behavior in underprivileged children [51].

In non-human primates, some of the brain systems described above (e.g., amygdala and raphe nucleus) (Figure 1) show increasing gray matter volumes with social status, but not with the size of the social network, possibly reflecting successful engagement in agonistic behavior [51,52] (Figure 3A, left). By contrast, cortical networks in which gray matter volume predicts both social status and network size (e.g., rostral DLPFC and STS) may be more related to the successful formation of social bonds that promote coalitions and social support [52,53] (Figure 3A, right). Yet, the correlational nature of these findings leaves open the important question of whether the identified brain areas are a cause or a consequence of social dominance, and the possible existence of mediating factors such as stress (see Neuropharmacology of Social Dominance Hierarchies: Clinical Implications section and see Outstanding Questions).

### Children's Understanding of Social Hierarchies

The neurobiology of the representations of social hierarchies remains to be investigated in children. Potential candidates include the brain systems described earlier for self–other social PE outcomes because they share common structures and mechanisms engaged with imitation; an early form of observational learning about actions [17] (Figure 2E). The intraparietal sulcus region, known to be engaged in rank comparisons in adults [17], is also likely to be engaged in children because it is involved in number comparisons and transitive reasoning in both adults and children [15,54–56] (Figure 1).

Although we know little about the neurobiological basis of social dominance representations in children, developmental psychologists have shown that preschoolers and even infants use various dominance-related cues such as body size to predict the outcomes of conflicts between social agents. For example, infants older than aged 8–13 months and  $\geq 10$  months were able to take this cue into account to predict the outcome of dominance contests between two agents aged 8–13 months and  $\geq 10$  months [57]. Prevailing in a physical conflict can also rely on social features such as the number of alliances with other in-group individuals. A recent study [58] has shown that infants as young as 6 months expected an agent from a numerically larger group to win a conflict against an agent from a smaller group. A possible reason why sensitivity to numerical size as a cue to dominance emerges earlier than body size is that it might be an even more salient ecological cue for a cooperative species [58]. To predict dominance, older children also use the face and body postures of social agents, as well as information about their wealth or age [59,60]. Yet, the developmental pattern of the understanding of these cues, as well as the influence of culture and family environment, still need to be clarified.

The early understanding of dominance does not only arise in the context of online cues that differentiate one agent from another. It also emerges through observational learning of past interactions between agents. For example, 15-month-old infants expect dominance relations to be stable over time and across situations: when they watch a dominant agent push a subordinate agent in order to monopolize an area, they expect the dominant agent to prevail over the subordinate agent, even when the conflict is of a different type [61]. However, human hierarchies

do not only rely on physical agonistic encounters. Verbal interactions, in which an individual imposes her/his will on another by giving orders and setting norms, also arise in the kindergarten [62]. Recent studies have shown that preschoolers can make explicit judgments of dominance through the observation of a wide variety of nonagonistic interactions. In particular, 3–5-year-old children judge that an individual is more likely to be the boss when that individual imposes their preference through persuasion or when they deny permission to use resources [60,63]. Developmental studies also indicate that sensitivity to more elaborate dimensions of hierarchy emerges at a later stage. Five-year-old, but not younger, children consider that being imitated and setting norms for others are signs of a powerful position [63,64].

The cognitive mechanisms that extract information from the observation of interactions do not only identify who is in the dominant and subordinate position. Knowing the ranks of other individuals may serve to make inferences about them and about the social structure of their group. A straightforward inference lies in predicting one dimension of the hierarchy from another, because in the social landscape several dimensions of hierarchy tend to correlate. Recent work has shown that preschoolers explicitly predict that an individual who gives orders to another will win a competitive game against the individual who complies and will have more resources than that individual [60]. A similar inference has also been observed with 17-month-old infants, who expected a dominant puppet to receive more resources than a subordinate puppet [65].

In groups of children as young as 2 years, dominance structures tend to be linear and transitive. That is, if A dominates B and B dominates C, A will likely dominate C. Knowing who is dominant between A and C could thus be achieved through **transitive inferences**. In large groups, transitive inferences may enable the representation of complete dominance structures by observing only a subset of the possible dyadic interactions. Animal research has established that many social species (such as fish, rodents, and birds) show the ability to make transitive inferences on the basis of dominance relations [66–69] (Box 3). Early developmental approaches viewed transitive reasoning as a domain-general ability that could hardly be acquired before 4 years of age [70]. However, recent studies using paradigms based on the presentation of dominance interactions showed that 10–15-month-old infants can actually make transitive inferences [71,72].

Dominance asymmetries can also influence social learning. Because dominant individuals are more successful in their groups, they might be perceived as more competent and more knowledgeable. Two recent studies have shown that preschoolers follow such heuristics [73,74]. In particular, in situations in which dominance interactions are implemented through physical or decisional power, preschoolers endorse the testimony of the dominant character more frequently than the testimony of the subordinate one. This also seems to indicate a positive evaluation of dominant individuals. However, as children grow older, they counteract dominance inequality by favoring subordinate individuals [75].

### Neuropharmacology of Social Dominance Hierarchies: Clinical Implications

Understanding the neurochemical processes involved in the emergence, maintenance, and consequences of social dominance hierarchies is crucial to improve our understanding of psychosocial disorders, including bullying in children. Recent neuropharmacological studies indicate a clear involvement of testosterone (Box 4), dopamine, and serotonin in social dominance in different species. These neuromodulatory systems might have been sculpted throughout evolution to facilitate high flexibility in social behaviors, as required in species forming dominance hierarchies [76]. Studying the neuropharmacology of social dominance relationships has important clinical implications because it contributes to the elucidation of the basic mechanisms underlying vulnerabilities to neuropsychiatric disorders, which are facilitated by the experience of repeated social defeats [77]. Such experience can trigger anxiety- and

depression-like symptoms, maladaptive social avoidance, behavioral inhibition, elevated glucocorticoids levels, higher vulnerability to addiction, and may even affect immune regulation in non-human primates [18,78,79]. Besides, neuropsychiatric disorders are largely treated by pharmacological modulation of these stress-sensitive systems.

Direct causal evidence for the implication of the dopaminergic system in encoding signals related to social hierarchies comes from recent optogenetics and neuropharmacological studies. Phasic optical stimulation of dopamine firing causes increased social avoidance and facilitates susceptibility to social defeats [80,81]. Moreover, higher dominance level or higher social status has been associated with higher striatal D2 receptor expression in both humans and monkeys [82–84] (Figure 3B). Consistently, the administration of a D2 antagonist, but not of a dopamine D1 antagonist attenuates social dominance in macaques and mice when the drug is given to high social class individuals, showing that D2 receptor signaling plays an important role in the maintenance of social hierarchy [85,86]. An important issue to be considered by future experiments will be to evaluate whether changes in dopamine signaling alter low level processes such as behavioral vigor [87] and effort perception [88], or whether they alter the representation of dominance relationships and the motivation to achieve dominance itself. Indeed, as discussed elsewhere [89], social dominance tests in animal research can be confounded by locomotor activity or motivation, and appropriate control experiments are sometimes lacking (but see [39]). Although there is currently no evidence in humans that a direct link exists between Blood Oxygenation Level Dependent (BOLD) responses to competitive outcomes and dopaminergic signaling, a recent rodent study combining optogenetics and fMRI suggests that this may be a case [90]. To validate this hypothesis in humans, combined positron emission tomography–fMRI imaging and imaging genetics will be useful tools [91,92].

Serotonin also plays a key role in the establishment of social hierarchies. One early study performed in groups of velvet monkeys showed that enhancement or suppression of serotonin signaling can respectively induce dominance or subordination in treated monkeys [93]. More recently, higher-ranked monkeys have been shown to demonstrate more gray matter in the dorsal raphe nucleus (DRN), which contains serotonergic neurons [52] (Figure 3A). Interestingly, dopamine neurons in the DRN show increased activity upon social contact following isolation, and the degree to which these neurons modulate behavior is predicted by social rank [94]. In mice susceptible to social defeats, optogenetic targeting has shown that social defeats engage DRN  $\gamma$ -aminobutyric acid (GABA) neurons and that postdefeat sensitization of these neurons decreases resilience to social defeat [95]. Moreover, preclinical studies have demonstrated that serotonin in the hypothalamus plays opposite roles in the regulation of male and

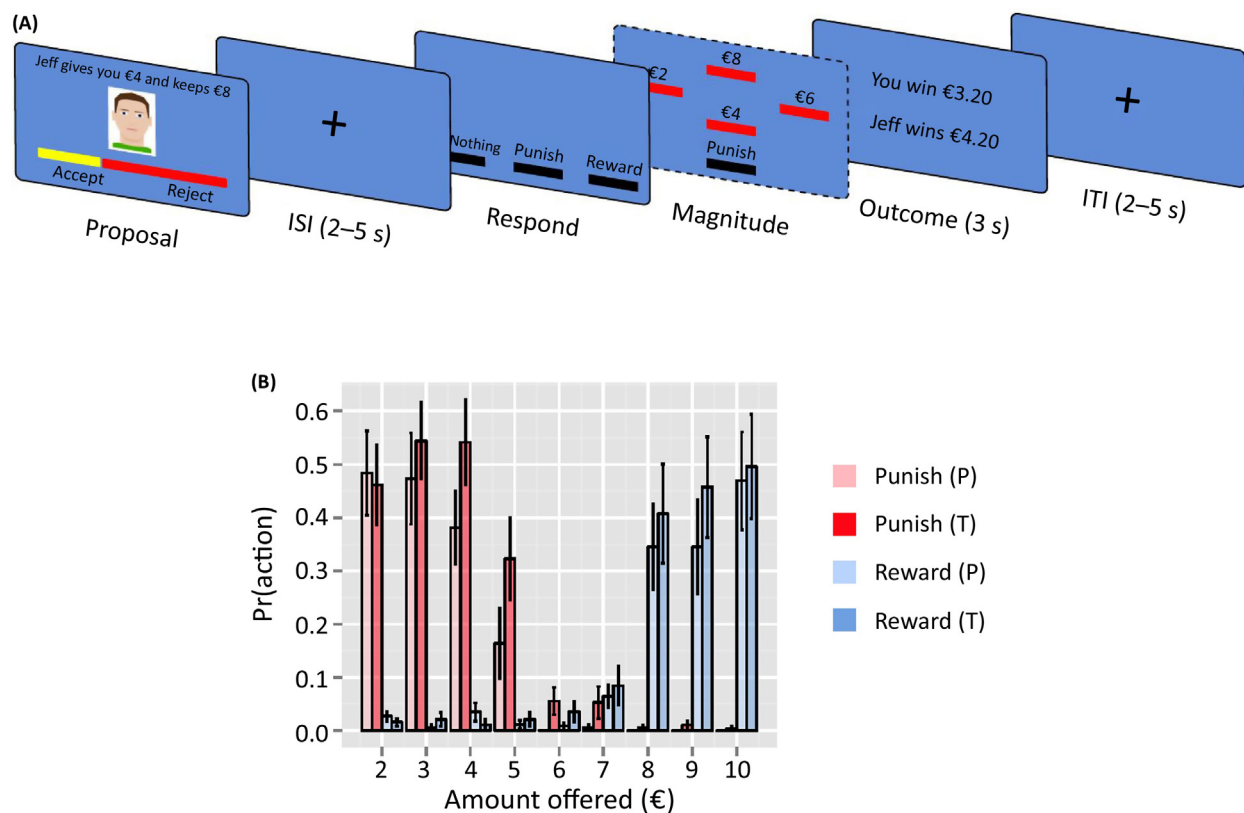
### Box 3. How Changes in the Environment Shape Expression of Social Hierarchies in the Brain

Understanding the relation between genetics and social behavior involves investigating the reciprocal links between changes in social information and modifications in brain function and behavior, including brain gene expression and long term epigenetic effects in various social species [76,119]. One important question is to understand how manipulation of social context or social interactions among individuals influences the brain at the neurophysiological and molecular level. For example, after removing the current dominant male from a group of a social fish (*Astatotilapia burtoni*), a subordinate male quickly starts to exhibit dominant behavior and displays changes in body coloration. After these behavioral changes a specific transcription-factor-encoding gene causally modifies the size and molecular responses of a group of gonadotropin-releasing hormone neurons in the preoptic area [76]. Thus, in *A. burtoni*, in which dominant males are reproductively competent while nondominant males are not, these neurons are not only crucial for reproduction – as in most species – but are also regulated by male social status, essential for establishing and keeping territories for reproduction. Social experience or changes in the environment are likely to trigger changes not in a single gene but in large gene networks in many brain regions at once. Interestingly, a recent study examining the expression profiles of neurochemical genes involved in the social decision-making brain network in >80 species across five vertebrate lineages found high overlap in many brain regions of this network [120]. In particular, the neurochemical gene expression profiles of investigated genes were completely conserved across vertebrates in the preoptic area and the basolateral amygdala.

## Box 4. Social Status Hypothesis of Testosterone

Testosterone plays a key role during social interactions. Although folk theories proposed that testosterone leads to increased **aggression**, a recent hypothesis is that testosterone is primarily involved in promoting behaviors intended to achieve and maintain social status or dominance [108,121]. This theory predicts that higher testosterone may indeed lead to increased aggression in social contexts where status is threatened by perceived provocation, while in other contexts, it may promote nonaggressive behaviors, such as generosity; more appropriate for advancing social status. Causal evidence for this social status hypothesis of testosterone comes from studies using tools from behavioral economics [122–125]. In a recent study, men injected with testosterone or placebo in a double-blind randomized design, played a modified ultimatum game as the receiver of a monetary split, which included the opportunity to punish or reward the offers of other players [123] (Figure 1). Administration of testosterone increased both the rates of punishment of low offers and the rates of reward of high offers. These results contradict a simple link between testosterone and male aggression, which would have predicted increased rejection and punishment of unfair offers and reduced reward of generous offers in participants injected with testosterone. Instead, depending on the social context, testosterone can cause prosocial behavior in males, thereby extending recent findings in women reporting that testosterone may have prosocial effects by increasing cooperation in the public goods game [126] and increasing generosity when repaying trust [122].

Thus, testosterone mediates different types of status-seeking behavior, increasing competitive or aggressive behavior with social challenges, and promoting prosocial behavior in the absence of these threats. Together, these studies indicate that some social challenges can lead to **reactive aggression**, but that aggressive behavior is not always adaptive in every situation. In the absence of these challenges or perceived threats to dominance, aggressive behavior may have detrimental effects on social standing. In such circumstances, dominance and high status seeking may be better served by displaying prosocial behavior.



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**Figure 1. Causal Evidence for Testosterone in Driving Status-Enhancing Behavior in Men.** (A) Participants accepted or rejected an offer to split a sum of money and then chose to punish or reward the proposer at a cost to themselves or do nothing. After an inter-stimulus interval, they specified the magnitude of punishment or reward. Finally, participants saw the net trial winnings of both players. (B) Treatment with testosterone increased rates of punishment of low offers and rates of reward of high offers. Adapted, with permission, from [123].

female dominance behaviors [96] (Figure 3C), which has important implications for many psychiatric disorders showing sex differences in their incidence and clinical course. In humans, evidence supporting a role of serotonin in social dominance is still sparse, but enhancing

serotonin levels through antidepressant medications or precursor of serotonin biosynthesis has been found to increase the frequency of dominance-related behaviors [97]. Future work combining fMRI and pharmacological manipulations are crucially needed to investigate dopamine, serotonin, and testosterone influences on the brain systems encoding social dominance and social network positions (see Outstanding Questions).

### Concluding Remarks and Future Perspectives

Decomposing the different processes engaged in the formation of social dominance hierarchies is a promising avenue that should offer mechanistic explanations for the emergence of interindividual differences at the behavioral and neurobiological level [20]. The neurocomputational mechanisms engaged when humans learn social ranks by observation or by direct competition are only beginning to be investigated, and this may be a fruitful research direction that could innervate different domains from developmental psychology to social neuroscience (see Outstanding Questions). Computational neuropsychiatry may also benefit from elucidating the dysfunctional neural mechanisms by which different clinical populations fail to learn social dominance relationships. In fact, the brain may not only use different learning algorithms when learning social hierarchies in noncompetitive or competitive situations [23–25] (Box 2), but it may also rely on distinct neuromodulatory circuits. Ultimately, the study of the brain processes underlying our ability to track dominance relationships and the role of neuropharmacological agents in these processes should contribute to the understanding of several neuropsychiatric disorders and may pave the way towards innovative therapeutic interventions.

One potential productive avenue for future research is to decipher whether the social environment can cause changes in dominance-related neural networks through changes in gene expression and, conversely, whether individual variation in neural networks and gene expression can predict dominance status. For example, an interesting fish model indicates that the social environment shapes the brain and alters the behavior of interacting animals by producing changes in gene expression in key brain nuclei [76] (Box 3). How the social environment causally influences gene expression and brain networks engaged in social dominance is an important question that will need to be investigated in primates.

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### Outstanding Questions

How does the motivation for occupying a high social rank change during development and across the lifespan? Are early individual differences found in infants' sensitivity for high social rank related to a similar sensitivity in adulthood?

Recent studies on children's understanding of dominance have used third-party tasks (allocentric representation). How and when do their representations of dominance emerge in self-referential situations?

Are the observed interindividual differences in the relationships between gray matter and social dominance a cause or a consequence of the social dominance? Are they present at birth or do they result from the social environment?

Social status changes in different contexts (e.g., we may be highly ranked as a chess player but low in our work hierarchy) and over time. How does our brain adapt to each context and what are the underlying neural mechanisms?

There are two types of social hierarchies: some are organizational (e.g., ranks in the army) and others are only related to higher skills in a specific domain. Do they differentially modulate grey matter in specific brain structures in humans?

Dynamics of social dominance relationships can be studied in animals with social network analyses. In humans, can we study these dynamics in the natural environment using the same tools?

Can we use electrical or magnetic stimulation of the mPFC in the context of tasks engaging learning social hierarchy mechanisms to improve disorders such as social anxiety or depression?

Are the brain networks engaged in social hierarchy representations transiently modulated by dopamine/serotonin/testosterone during social interactions?

Do dopamine neurons encode social prediction errors as nonsocial ones? How do dopamine and serotonin



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neurons respond to conspecifics of different social ranks? Do they implement fight or flight decisions?

Repeated social defeats are key to establishing subordinate ranks in animals during competitive dyadic interactions. What are the exact neurobiological consequences of repeated social defeats in the emergence of neuropsychiatric disorders in humans?

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