CHAPTER

17

Social Dominance Representations in the Human Brain

R. Ligneul, J.-C. Dreher

Institute of Cognitive Science (CNRS), Lyon, France

Abstract

Social dominance refers to relationships wherein the goals of one individual prevail over the goals of another individual in a systematic manner. Dominance hierarchies have emerged as a major evolutionary force to drive dyadic asymmetries in a social group. Understanding how the brain detects, represents, implements, and monitors social dominance hierarchies constitutes a fundamental topic for social neuroscience as well as a major challenge for the future of clinical psychiatry. In this chapter, we argue that the emergence of dominance relationships is learned incrementally, by accumulating positive and negative competitive feedback associated with specific individuals and other members of the social group. We consider such emergence of social dominance as a reinforcement learning problem inspired by neurocomputational approaches traditionally applied to nonsocial cognition. We also report how dominance hierarchies induce changes in specific brain systems, and we review the literature on interindividual differences in the appraisal of social hierarchies, as well as the underlying modulations of the cortisol, testosterone, and serotonin/dopamine systems that mediate these phenomena.

INTRODUCTION

Social Hierarchies in Health and Well-Being

Social dominance refers to situations in which an "individual or a group controls or dictates others' behavior, primarily in competitive situations" [1,2]. Social dominance hierarchies influence access to resources and mating partners and therefore constitute a potent biological force binding together social behavior, well-being, and evolutionary success. The concept of social dominance is most often applied to "learned relationships," shaped by a history of social victories and defeats within dyads of individuals [3]. Together with other forms of power, social dominance asymmetries constitute a pivotal concept for understanding social organizations and predicting individual behaviors.

Many animal studies indicate that iterated social defeats can trigger maladaptive social avoidance, behavioral inhibition, elevated glucocorticoid levels, and higher vulnerability to addiction, anxiety, or depression [4–7]. Epidemiological approaches in humans have subsequently confirmed that suffering from a chronically low socioeconomic status or enduring transient status-lowering threats facilitates both somatic and psychiatric disorders [8,9]. Unfortunately, it has long been difficult to disentangle the specific contributions of stress, socioeconomic status, and social dominance on the human brain. In particular, very little is known about the cerebral mechanisms governing the progressive establishment of social dominance hierarchies and associated neurobehavioral changes through real-life interactions (for a review of such mechanisms in nonhuman primates and of genetic mechanisms in zebra finches, see Chapters 15 and 28).

In this chapter, we will first consider the learning of social dominance as an incremental process, allowing us to develop a neurocomputational approach to a key decision problem (i.e., to initiate or not a competitive interaction). Second, we will review important interindividual differences that naturally derive and influence social dominance hierarchies. Third, we will highlight the tight relationship of social dominance with stress and neuroplasticity [6] by reporting its effects on the hypothalamic–pituitary–adrenal (HPA)/hypothalamic–pituitary–gonadal (HPG) axes as well as on the serotonin and dopamine systems [10].

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Social Hierarchies as a Major Evolutionary Pressure and Pivotal Feature of Societies

In folk psychology, dominance is often considered a fundamental motive of social organisms. However, while many primatologists agree that social ranks correlate positively with offspring production in many primate and nonprimate species, effect sizes are usually small and many counterexamples exist, indicating that subordinate individuals often achieve decent reproductive success [11,12]. Moreover, dominance hierarchies spontaneously reemerge, even if only subordinate or only dominant individuals are put together to form a new social group at each generation [13,14], implying that the social environment dynamically tunes individuals' brains to promote the best behavioral strategy given the social context, through synaptic and epigenetic plasticity mechanisms. Dominance and subordination can thus be better described as life-history strategies [15,16], because both constitute adaptations to the social environment and both can increase evolutionary fitness.

The importance of social dominance for domain-general cognition is primarily rooted in the so called "social brain hypothesis," which stipulates that the need to optimize behavior within complex social environments largely constrained the evolution of the primate brain. This theory was first outlined in the pioneering study of Alison Jolly in lemurs [17], and it was popularized by Humphrey [18], Byrne and Whiten [19], and Dunbar [20], who provided correlational evidence for the coevolution of social complexity and various markers of brain development. In evolved animals, other group members constitute stochastically behaving entities guided by hidden mental states and obeying complex sets of rules. Consequently, predicting their actions and improving our transactions with them requires very elaborated computations which have long been overlooked in cognitive neurosciences. A similar argument also applies to simpler behaviors: the neural mechanism that enables human subjects to avoid selecting a blue square associated with electric shock delivery in the lab might have partly been sculpted, throughout evolution, to enable efficient avoidance of aggressive dominant individuals within one's social group. The possibility that "social life provided the evolutionary context of primate intelligence" [17] is thus key to foreseeing the importance of social dominance for domain-general, high level human cognition.

Previously, a large neural circuit activated when people make decisions in social settings has been identified using functional magnetic resonance imaging (fMRI) in humans. Key components include the orbitofrontal cortex, the ventromedial prefrontal cortex (VMPFC), the dorsomedial and dorsolateral prefrontal cortex (DLPFC), parts of the superior temporal sulcus (STS) including a region near the temporoparietal junction (TPJ), and the anterior cingulate gyrus. In sum, there is now extensive evidence that social decision-making relies on many "nonsocial" subcortical and brain stem circuits. Social decision-making also overtakes the canonical cortical network of social cognition encompassing the medial prefrontal cortex (MPFC), the STS, and the TPJ (Fig. 17.1A).

Since 2005, a number of fMRI studies have investigated the perception of social ranks based on noncompetitive cues, such as wealth [23,24], postures [25], uniforms [23], facial traits [26], and celebrity, height, or intelligence [27,28]. Completing the pioneering work of Zink et al. [29], these studies have also demonstrated the engagement of a large brain network involved in social hierarchy processing, including the amygdala, hippocampus, striatum, ventrolateral prefrontal cortex (VLPFC), rostromedial prefrontal cortex (RMPFC), inferior parietal lobule (IPL), and the fusiform gyrus (Fig. 17.1B–C). Although these perceptual processes linked with social dominance raise many important questions (for a review see [30]), we will focus in this chapter on the neurocomputational processes that underlie the *learning* of social dominance statuses (SDSs).

LEARNING SOCIAL DOMINANCE HIERARCHIES

In what follows, we will propose that *one's own* dominance status is learned incrementally by accumulating the numerous competitive feedbacks (victories and defeats) obtained against other group members. Put simply, individuals who experience on average negative feedback following competitive encounters will develop an adaptive subordinate profile, which may take them away from social conflicts by promoting submission, and vice versa for dominant individuals. Importantly, the same principle can also be applied to the rapid update of *others'* SDS during competitive interactions. These assumptions allowed us to develop a neurocomputational approach to characterize the emergence of social dominance relationships through time and provide computational neuroscientists with an adequate framework to test quantitative and mechanistic hypotheses about this process [21,31].

Reinforcement Learning Approaches to Social Cognition

Mathematical models are increasingly used in social neuroscience as they can probe, simultaneously, several cognitive processes which would otherwise not be separable [21,31] (see also Chapters 18 and 19). Three main

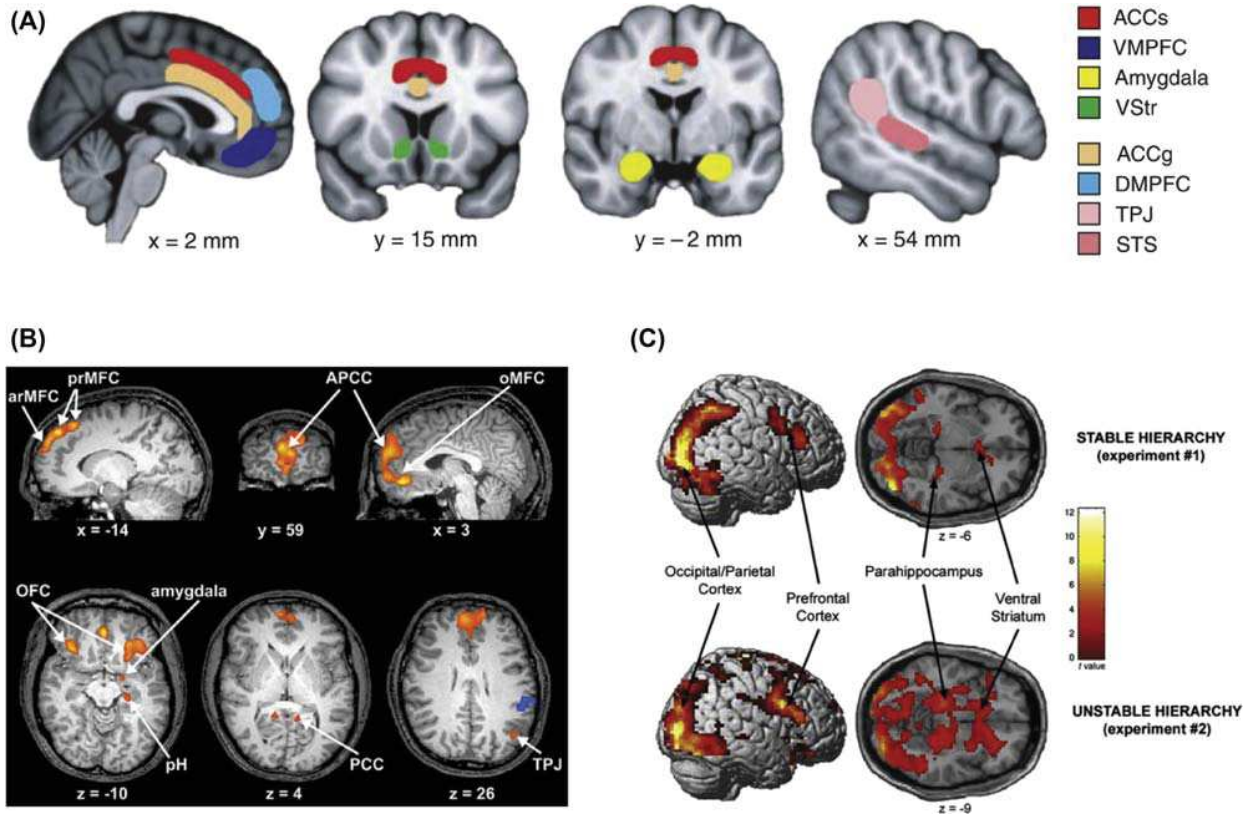

FIGURE 17.1 (A) **The functional neuroanatomy of social behavior**. Primary colors denote brain regions activated by reward and valuation, frequently identified in studies of social interaction within the frame of reference of the subject's own actions: anterior cingulate cortex sulcus (*ACCs*), ventromedial prefrontal cortex (*VMPFC*), amygdala, and ventral striatum (*VStr*). Pastels denote brain regions activated by considering the intentions of another individual: anterior cingulate cortex gyrus (*ACCg*), dorsomedial prefrontal cortex (*DMPFC*), temporoparietal junction (*TPJ*), and superior temporal sulcus (*STS*). *(From Behrens TEJ, Hunt LT, Rushworth MFS. The computation of social behavior. Science 2009;324:1160–64, with permission.)* (B) **Cerebral substrates of social comparison processes**. Comparative judgments about the height or the intelligence of others activate specifically the anterior prefrontal cortex, the amygdala, and the TPJ. *(From Lindner M, Hundhammer T, Ciaramidaro A, Linden DEJ, Mussweiler T. The neural substrates of person comparison—an fMRI study. Neuroimage 2008;40:963–71, with permission.)* (*APCC*, anterior paracingulate cortex; *prMFC*, posterior medial prefrontal cortex; *arMFC*, anterior portion of the rostral medial frontal cortex; *OFC*, orbitofrontal cortex; *oMFC*, orbital medial prefrontal cortex) (C) **Statistical maps of the brain regions more engaged in the comparison "superior player > inferior player."** Compared to inferior individuals, the perception of superior individuals elicited stronger activations in many brain regions including the dorsolateral prefrontal cortex, the medial prefrontal cortex, the striatum, and the occipitoparietal cortices. *(From Zink CF et al. Know your place: neural processing of social hierarchy in humans. Neuron 2008;58:273–83, with permission.)*

subsystems have been unraveled by this approach: the VMPFC, together with the ventral striatum, may be responsible for observational learning and reward prediction error signaling [32,33]. Second, the anterior cingulate cortex, the DLPFC, and the IPL may compute prediction errors elicited when others' behaviors deviate from our predictions about them. Third, the RMPFC and TPJ/posterior STS may compute the updating of one's own and others' mental states, [33,34] as well as the degree of interpersonal influence during social interactions, that is, the degree to which one's own actions and utilities are determined by others' skills and strategies [35].

Within iterated competitive games, rmPFC activity was often shown to encode second-order variables (i.e., variables inferred from other learned variables) [31,34,36]. For example, in the inspector game or in the matching pennies task respectively used in Hampton et al. [34] and Seo et al. [36], a player able to take into account the influence of his or her past choices over the evolution of another's strategy will be able to increase his or her chances of winning to the detriment of the other, because this second-order information enables the player to better predict the other's choice (see Chapter 18 from Lee et al.). Given that the ability to control others' behaviors and outcomes is at the core of the social dominance concept, it would be tempting to characterize such player as "mentally dominating" his or her opponent. Interestingly, if the "subordinate" opponent starts to play on a purely random basis, the opportunity for interpersonal control disappears, possibly contributing to the frequency of inconsistent or irrational social behaviors in humans. Moreover, the consequences of

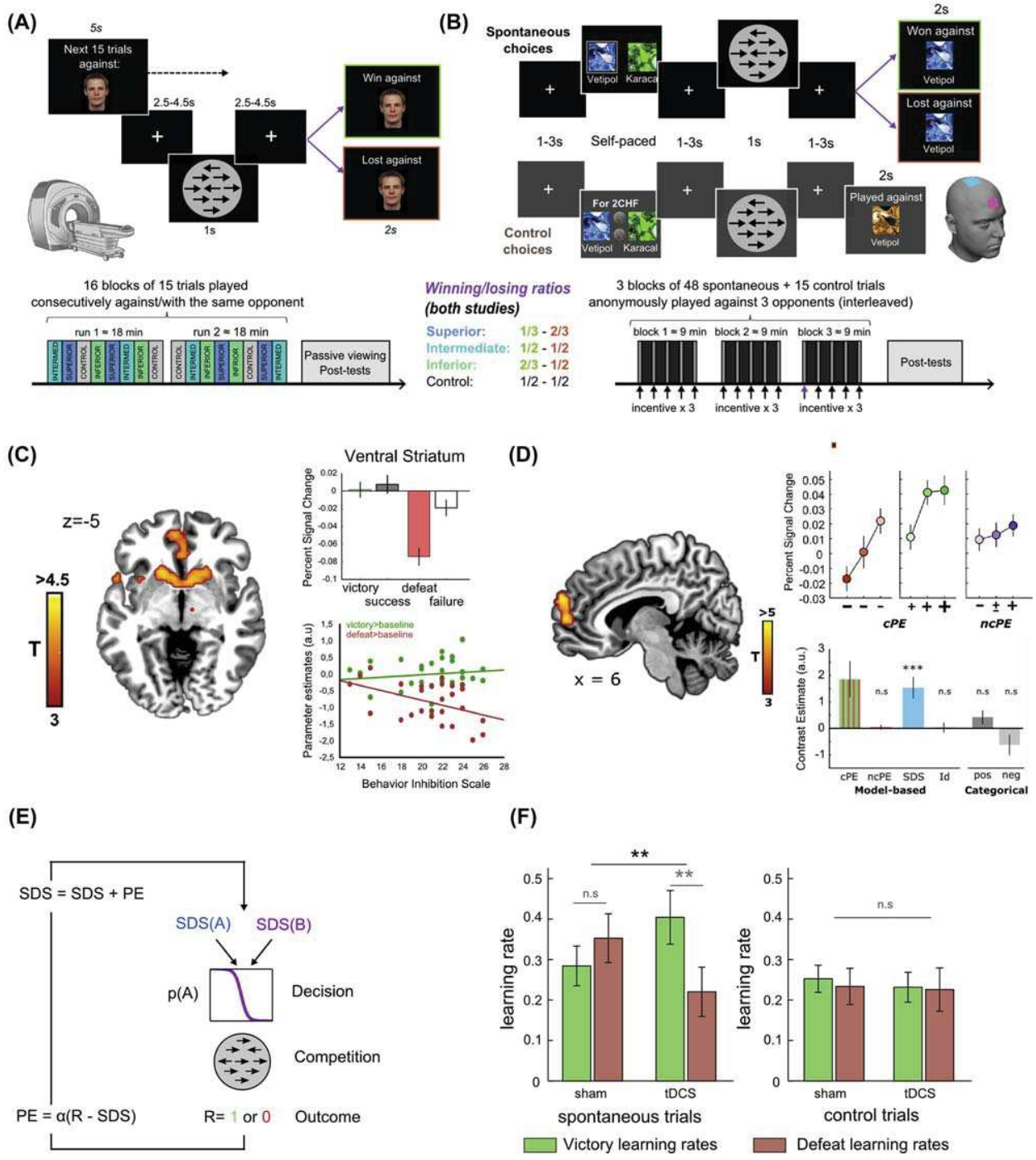

FIGURE 17.2 **The emergence of social dominance through reinforcement learning**. (A) **Typical trial and experiment time courses for the fMRI experiment**. During 15 trials of a "miniblock," subjects played against (or with) the same player in the competitive (or control) situation. The competitive task required subjects to evaluate a series of *stationary arrows*, indicating which direction the majority of these *arrows* pointed (*left or right*). The task was performed against one of three virtual opponents implicitly associated with three frequencies of winning and losing. To succeed in the competition, subjects were instructed to answer accurately and faster than their opponent. (B) **Typical trial and experiment time courses of the brain stimulation experiment**. Subjects performed a similar perceptual task but now opponents were marked by visual symbols and artificial names rather than a face photograph. Subjects could now choose which opponent to defy among two alternatives (three opponents per block), in two types of trials designed to distinguish dominance-based (spontaneous) and reward-based (control) choices. In half of the subjects, the rostromedial prefrontal cortex (RMPFC) was monitored with the excitatory anodal electrode of the transcranial direct current stimulation (tDCS) apparatus (magenta; the reference electrode on the vertex is in blue). (C) **Striatal encoding of competitive defeats**. Competition-specific outcome signals revealed by the interaction competitive victory and control failure > competitive defeat and control success

this interaction between social dominance and mentalization of interpersonal influence within strategic games has also been explored based on evolutionary reinforcement learning models [37], which showed that mentalizing abilities may indeed promote social status when the rate of cooperation among group members is low.

Finally, neuroimaging studies indicate that the RMPFC (as well as the TPJ and the medial STS) is generally more engaged when subjects are invited to compete against other humans compared to computers [29,38,39,40–42], suggesting that the RMPFC might be involved in representing the mental states of others and/or the dominance relationship emerging between two individuals. Competitive interactions also tend to lead to higher activity of the RMPFC compared to cooperative interactions, which indicates a possible competition specificity of the cognitive processes implemented in this structure [40,43].

The Emergence of Dominance and Subordination by Reinforcement Learning

According to the pioneering theory of Bernstein [3], dominance relationships are learned progressively, by integrating the positive and negative competitive feedback associated with specific individuals and other members of the social group taken as a whole. A competitive outcome thus provides information about others' behaviors (which underlies the representation of objective social hierarchies) and information about oneself (which may lead to adjustments in subjective social status and related variables such as self-esteem). In other words, the former information may foster target- or dyad-specific dominance behaviors while the latter may foster target-independent behavioral profiles of dominance and subordination with individuals. Although both can be described by a similar reinforcement learning scheme, the time constants (and learning rate) associated with those two processes might be different, as self-representations intuitively appear less volatile than representations about others, in most people.

By learning social dominance representations, individuals can anticipate their probability of winning versus losing and therefore decide whether they should carry on fighting or disengage from a confrontation in order to limit the physical and social costs associated with a defeat. Outside of agonistic interactions, monitoring such probability can also prevent the escalation of social conflicts for which the risks of losing outweigh the expected benefits of winning. Interestingly, in the cost–benefit trade-off that underlies the decision to compete against another conspecific, the cost is typically associated with a property of the opponent (i.e., his or her strength or skill, which translates into a given probability of losing and a given effort to be exerted when trying to win), whereas the benefit usually refers to the external resource at stake (a notable exception being social competitive play, in which no such external incentive is present). The anticipated energy costs associated with competitive interactions and external resources motivating the social conflict are thus pivotal to making optimal decisions. Yet we will here restrict the problem to winning-losing probability estimation, which already provide strong empirical evidence to the aforementioned reinforcement-learning model.

In a recent study, we have induced an implicit dominance hierarchy in men through a competitive game involving three opponents of different strengths, complemented by a noncompetitive control condition (Fig. 17.2A). Using fMRI, we first observed specific responses to social defeats in the ventral striatum and other subcortical regions, which were correlated with trait inhibition across subjects (Fig. 17.2C; see also "Interindividual Differences Resulting From Social Status and Personality"). Second, and more importantly, model-based analyses highlighted the functions of the rostromedial cortices in tracking the dominance status of opponents (i.e., anticipated winning-losing probabilities). More specifically, the RMPFC encoded opponent-specific prediction errors and appeared to monitor the probability of winning against each player in a dynamic fashion, throughout the competitive task (Fig. 17.2D).

These findings were obtained by applying a classical Rescorla–Wagner rule [Eq. (17.1); Fig. 17.2E] tracking

were observed in the bilateral ventral striatum. The amplitude of defeat-related deactivations was correlated with the behavioral inhibition personality trait across subjects. (D) **Encoding of competitive prediction errors (cPE) in the RMPFC**. Analyses showed that the activity changes observed in the RMPFC encoded a signed competitive prediction error, which did not reflect winning or losing per se, the identity of the opponent, or interactions of these two factors. ncPE, noncompetitive prediction error; SDS, social dominance status (*Id*, opponent type). (E) **Overview of the computational model**. Our reinforcement learning algorithm assumed that decisions are taken probabilistically (softmax policy) according to the value of each available opponent. Once the competition occurred, the value of the selected opponent was updated for the next trial proportional to the prediction error elicited by the outcome [i.e., ($R - \text{SDS}$) with victory $R = 1$ and defeat $R = 0$] multiplied by the learning rate α. (F) **Effects of RMPFC tDCS on the parameters governing social dominance learning**. Whereas average learning rates related to defeats and victories were balanced in the sham group, stimulating the RMPFC using anodal tDCS induced a significant imbalance in the learning rates, with more weight placed on victories and less weight place on defeats. *From Ligneul R, Obeso I, Ruff CC, Dreher JC. Dynamical representation of dominance relationships in the human medial prefrontal cortex. Current Biology, in press.*

the probability of winning in such agonistic interactions, by simply initializing P_{win} (or SDS) at 0.5 and monitoring the outcome R (0 for defeat, 1 for victory);

$$SDS(t+1) = SDS(t) + \alpha * (R - SDS(t)) \quad (17.1)$$

The prediction error term $R-SDS(t)$ multiplied by the learning rate α allows updating the anticipated chances of winning (or SDS) in the next encounter at $t+1$. Also called momentary social dominance status, or SDS, this "probability estimate could then be used to decide whether one should defy another conspecific, according to a decisional policy such as the probabilistic softmax rule. In real-life competitive settings, when the chances of winning are deemed too low to initiate or continue the fight, the decision-maker may start to submit, hence meeting the criterion of a dominance relationship [3,44]. Moreover, generalizing or averaging of target-specific SDSs over all members of the group would naturally underlie the emergence of chronically dominant or subordinate personality profiles.

Next, using an adapted version of our competitive perceptual decision-making task (Fig. 17.2B), we demonstrated that transcranial direct current stimulation (tDCS) applied over the RMPFC exerted a causal influence over social dominance learning, reflected in higher learning rates associated with victories and lower learning rates associated with defeats (Fig. 17.2F). This result paralleled a study in mice in which viral injections, producing an increase or decrease in overall MPFC activity, led to increases or decreases in the dominance ranks of animals [45].

In the past, it has been difficult to ascertain whether neural network covarying with learning of social dominance was a cause or a consequence of the emergence of social dominance in humans although original experiments in animals suggested a profound impact of dominance on brains and bodies. For example, it was shown that selective lesions of the amygdala or the administration of a serotonergic antidepressant can induce changes in the behavioral expression of dominance in monkeys [46,47] and human patients with lesions of the MPFC are also impaired in their ability to make social dominance attributions based on the narrative description of diverse social interaction [48]. Beyond those classical findings, brain stimulation techniques such as tDCS shall thus constitute an important tool for the study of causality in fine-grained social dominance behaviors among healthy human subjects.

INTERINDIVIDUAL DIFFERENCES AND SOCIAL DOMINANCE

Cognitive neuroscientists tend to rely on the convenient assumption that human brains are largely similar across genders, ethnicities, sexes, ages, and social groups. This assumption facilitates the generalization of observations typically made in a few dozens of students to the whole human population or, at least, to the whole student population. Impeding predictive power and reproducibility of empirical findings, this assumption is unfortunately often invalid. Therefore, the systematic study of interindividual differences has begun, so that many neuroscientists now routinely report differences in personality traits, gray matter volumes, functional activities, or connectivity estimates to better explain the behavioral variability of their subjects [49]. In this perspective, social dominance holds a strong potential to explain variability observed within social groups, which would otherwise be envisioned as homogeneous (such as psychology students participating in social learning experiments). Indeed, the study of social dominance promises more than simply *accounting* for interindividual differences in behavior and physiology: it may also offer mechanistic explanations for the *emergence* of neural, behavioral, cognitive, and social variability. For example, the existence of clear-cut dominance hierarchies in pure strains of rodents (i.e., genetically identical) stresses that the behavioral and physiological features of dominant and subordinate animals derive largely from experience and adaptation. Moreover, although social dominance is a universal principle structuring social groups, it is also highly dependent on the culture, the gender, and the personality of the participants.

Intercultural Differences in the Appraisal of Social Dominance

Human cultures vastly differ in how they value personality traits related to social dominance. For example, the construction of self in collectivistic east Asian cultures tends to be more interdependent upon other group members than in individualistic societies in which the construction of self appears more as a quest for independence and autonomy with respect to other group members [50]. As Sedikides et al. [51] wrote, "in individualistic cultures, the relevant dimension [of self-construal] is agency, defined as a concern with personal effectiveness and social dominance. In collectivistic cultures, however, the relevant dimension is communion, defined as a concern with personal integration and social connection." Acknowledging cultural differences in the promotion of *person-centric* versus *normative-contextual* models of self-construal is thus crucial to avoid a partial, Western-centric conception of behaviors related to social dominance. For example, an influential study demonstrated that European American children are more motivated to solve anagrams when they could choose the category of problem to be solved

compared to when their mother or the experimenter chose it for them, whereas Asian American children displayed the opposite pattern [52]. This finding indicates that, early in development, the motivational attitudes toward dominant others (here, the experimenter or the parent) vary greatly across cultures. It is also consistent with the fact that high external locus of control (i.e., the feeling that one's own life is controlled by others) is much more strongly correlated with trait anxiety and negative emotions in individualistic compared to collectivistic societies [53].

In the only available neuroimaging study (as of this writing) probing intercultural differences in the appraisal of social dominance (Fig. 17.3A), Freeman and coauthors demonstrated that the neural correlates of social dominance expressed by body postures were reversed in the ventral striatum and the MPFC when comparing American (more activity in response to dominant postures) and Japanese subjects (more activity to subordinate postures). Interestingly, these responses to dominant and subordinate postures were also correlated with the behavioral tendency of the subjects: a stronger response to dominant postures predicted (self-reported) dominant behaviors typical of Western cultures, whereas a stronger response to subordinate cues predicted the opposite behaviors. Although we firmly believe that most of those

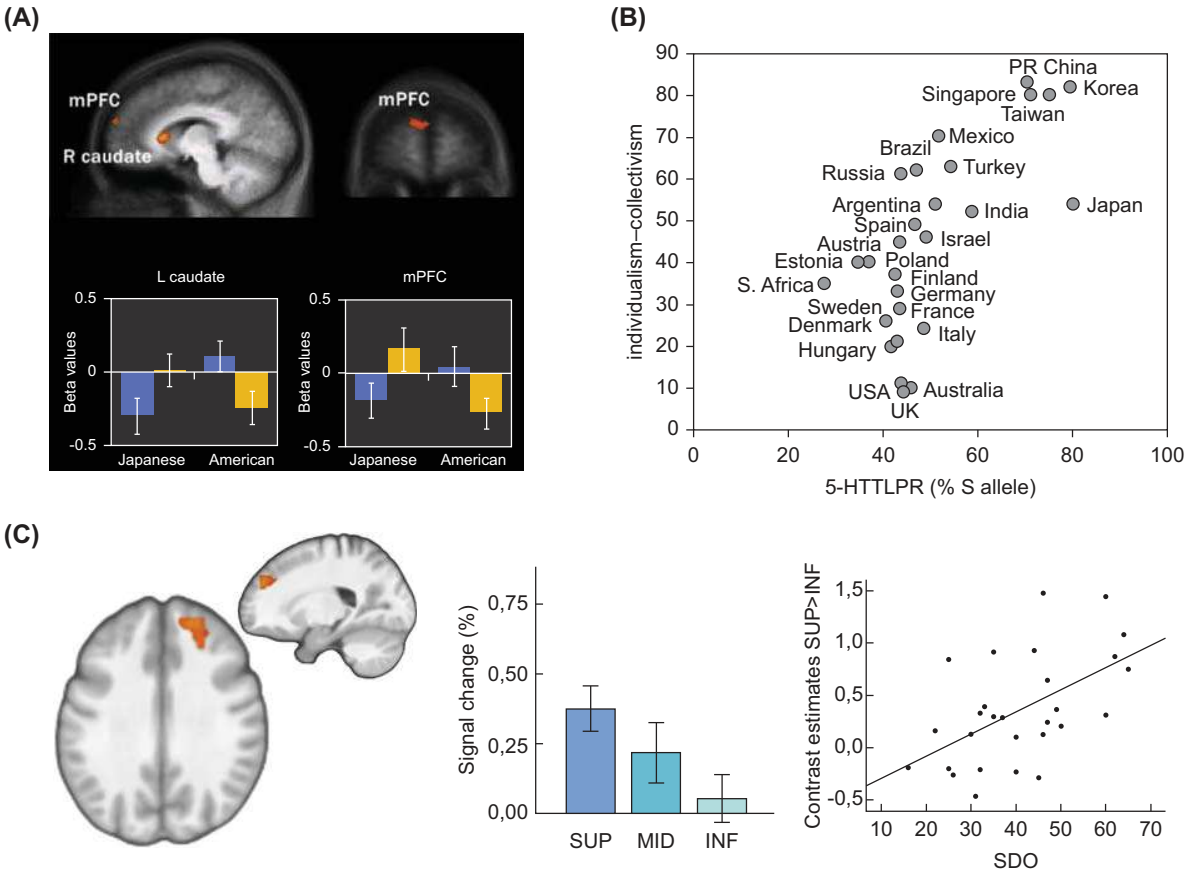

FIGURE 17.3 **Brain-related interindividual differences in the appraisal of social hierarchies**. (A) **Whole-brain analysis testing a status display × culture interaction effect**. In Americans, the medial prefrontal cortex (*mPFC*) and the caudate nucleus exhibited reliably stronger blood oxygen level-dependent (BOLD) responses to dominant stimuli relative to subordinate stimuli; in the Japanese, these same regions exhibited the opposite pattern, showing reliably stronger BOLD responses to subordinate stimuli relative to dominant stimuli. *(From Freeman JB, Rule NO, Adams RB, Ambady N. Culture shapes a mesolimbic response to signals of dominance and subordination that associates with behavior. Neuroimage 2009;47:353–59, with permission.)* (B) **Correlation analysis between Hofstede's individualism–collectivism index and frequency of S allele carriers of 5-HTTLPR across 29 nations**. Collectivistic nations showed higher prevalence of S allele carriers. *(From Chiao JY, Blizinsky KD. Culture-gene coevolution of individualism–collectivism and the serotonin transporter gene. Proc Biol Sci 2010;277:529–37, with permission.)* (*5-HTTLPR*, serotonin-transporter-linked polymorphic region). (C) **The relationship between political orientation and the neural sensitivity to competitive ranks**. In one of our experiments, the right anterior dorsolateral prefrontal cortex encoded social rank as induced by a prior competitive task against three opponents. In addition, the sensitivity of this brain region to social rank was strongly correlated with the social dominance orientation across subjects, thereby indicating that subjects more prone to legitimizing and reinforcing social inequalities are also more sensitive to competitive hierarchies [67]. *INF*, inferior; *LPP*, late positive potential; *MID*, middle; *SDO*, social dominance orientation; *SUP*, superior; *tDCS*, transcranial direct current stimulation.

inter-individual differences derive from the reinforcement-learning process described above, a cross-cultural genetic analysis revealed that endogenous serotonin reuptake capacity covaried with the individualistic–collectivistic opponency and the steepness of social hierarchies from one country to another (Fig. 17.3B) ([54]; see also "Dopamine, Serotonin, and Social Hierarchies in Rodents and Nonhuman Primates"). Located in the promoter region of the serotonin transporter, this polymorphism is also predictive of stress-coping strategies and resilience [55]. Cross-cultural differences in the perception of social dominance may thus be partly based on polymorphisms of genes engaged in serotoninergic (but also dopaminergic) transmission. Yet, as we will see, these polymorphisms may actually act by altering the learning process which is a the core of social dominance relationships.

Interindividual Differences Resulting From Social Status and Personality

By definition, the existence of a social dominance hierarchy means that different members of a given group experience different social environments and attribute different motivational values to specific social behaviors. Social hierarchies define the type of social dilemma most often faced by individuals and the range of options available to solve them. Thus, it is reasonable to expect that different social ranks would turn into different patterns of brain activity and—possibly—different brain anatomies.

A paper by Noonan, Sallet, Mars, and coauthors studied 36 macaques living in groups of two to seven members in which social dominance hierarchies could be reliably assessed [56] (see also Chapter 15). Their analyses showed that gray matter volumes markedly and reproducibly differed in several brain regions as a function of social rank. Higher ranked animals had more gray matter in the hippocampus, the amygdala, and the serotonergic brainstem, as well as in the medial temporal sulcus and the rostral prefrontal cortex. Because the last two were also correlated with the size of the group in which those animals were housed, the authors suggested that they might be "linked to the social cognitive processes that are taxed by life in more complex social networks and that must also be used if an animal is to achieve a high social status." In addition, lower ranked animals had more gray matter in three regions of the basal ganglia involved in habit learning and aversive processing: the dorsal striatum, the caudate nucleus, and the posterior putamen. As of this writing, the exact mechanisms that drive these correlations are unclear, but the ability of endogenous and drug-induced serotonin release to alter gray matter volumes and/or to stimulate neurogenesis in several brain regions offers promising perspectives [57,58]. In addition, the pervasive effects of chronic stress on brain circuitry should be taken into account, as it is well known that subordinate individuals tend to be more stressed than dominant individuals and more prone to develop stereotypical behaviors, especially in captivity settings (see "Stress Asymmetries Paralleling Social Hierarchy Rank Have Adverse Consequences on Adrenocortical, Reproductive, and Neural Systems").

In humans, the existence of neuroanatomical correlates of social ranks per se remains underexplored. Some developmental neuroimaging studies indicate that, even after correction for several confounding factors, higher parental socioeconomic status still predicts higher prefrontal cortical thickness in children [59] and increased gray matter volumes in several brain regions, including prefrontal but also occipital, parietal, and limbic areas [60]. Behavioral sensitivity to social dominance expressed by facial traits or induced by competitive games may also be predicted by neuroanatomical variations in the insula and other regions [61,62].

In addition to the (sustained) neuroanatomical signature of social hierarchies, humans also *process* social events differently, depending on their own social standing. For example, Ly and coauthors demonstrated that low-status subjects had stronger striatal responses when presented with low-status faces, whereas the opposite was true for high-status subjects [63]. In one of our experiments [64], we found that the sensitivity of the ventral striatum to social defeats in a competitive perceptual decision-making game was correlated with the behavioral inhibition personality trait [65], often linked with social subordination and anxiety [66]. Because more inhibited individuals had more salient deactivations in response to defeats in this structure, one could infer that the repeated experience of social defeats not only lowers social status and social dominance, but also heightens the overall sensitivity of the motivational system to threats and negative events (Fig. 17.2C). Moreover, in another experiment [67], we observed that the sensitivity of the right anterior prefrontal cortex to social rank of neutral faces was strongly correlated with the Social Dominance Orientation questionnaire (Fig. 17.3E), which reflects the degree to which one envisions social hierarchy and economic inequalities as legitimate and necessary phenomena [68]. Deciphering the neurocognitive mechanisms involved in the appraisal of social hierarchy may thus help us understand real-world political divides [69].

NEUROCHEMICAL APPROACHES TO SOCIAL DOMINANCE AND SUBORDINATION

The neurochemical processes involved in the emergence, maintenance, and consequences of social

dominance hierarchies by reinforcement-learning are key to translating fundamental social neurosciences into new therapeutic options and to improve our understanding of psychosocial disorders. Those disorders are largely mediated by pharmacological modulation of plastic, stress-sensitive systems such as hormonal and monoaminergic signaling. All "culture-like" features of animal societies can influence the dynamical form taken by a social hierarchy and the manifold individual profiles composing it. Nonetheless, the hormonal and neural systems that underlie the variable expressions of dominance across species, groups, and individuals have been highly conserved through evolution. Consequently, the acute and long-term consequences of social defeats are now widely studied because of their ability to trigger robust anxiety- and depression-like symptoms in animals, thereby providing a useful translational model of affective disorders [70].

Stress Asymmetries Paralleling Social Hierarchy Rank Have Adverse Consequences on Adrenocortical, Reproductive, and Neural Systems

In the attempt to explain dominance hierarchies in rodents, nonhuman primates, and humans, cortisol and testosterone have long played the first roles. Relatively easy to quantify, they reproducibly covary with social rank across species and experimental conditions. They are often jointly investigated because they interact at the physiological and behavioral levels. Cortisol and testosterone are the end products of two hormonal axes reciprocally inhibiting each other: the HPA axis and the HPG axis, respectively [71,72] (Fig. 17.4A). Moreover, exposure to stressors activates a chain of endocrine reactions, including secretion of glucocorticoids by the adrenal glands, which reallocate energy resources necessary to adapt rapidly to the stressor. In the long term, high levels of glucocorticoids can however disrupt an essential negative feedback loop, hence leading to immune function suppression as well as impairments in hippocampal and prefrontal functioning [73,74]. On the other hand, testosterone largely contributes to muscle mass, male secondary sexual characteristics, and reactive aggressive behaviors, which are relevant to predict the onset and the outcome of agonist interactions [6,72].

Modern ethology has reported a great variability between and even within species, regarding whether high- or low-ranking animals are the ones who are the most stressed in a dominance hierarchy. Many factors influence such rank-associated stress in stratified mammalian societies. Such factors include, but are not limited to, species-level variations in style of breeding system (cooperative/competitive), social and mating systems, housing, despotic versus egalitarian hierarchy style [75], and hierarchy stability within species [76]. In despotic hierarchies, resource access is skewed markedly and dominant positions are attained through aggression and intimidation, whereas in "egalitarian" hierarchies resource distribution is more equal and dominance is attained with the support of subordinate individuals. A general concept to help resolve these differences in the relationship between rank and stress across species is that it is the rank that experiences the most physical and psychological stressors that tends to display the most severe stress-related response.

In primates, glucocorticoid levels are often higher in subordinate males whenever a dominance hierarchy is stabilized and testosterone levels are generally independent of social rank [76,77]. However, higher-ranking males tend to experience higher testosterone and glucocorticoid (stress hormone) levels than lower-ranking males whenever their dominance rank is threatened (i.e., in a period of social instability) [76,77]. Together with the impact of living conditions (i.e., captivity, semi-captivity, free ranging, access to resources, size of the groups, etc.), this phenomenon probably explains the variability in empirical findings between and within species regarding whether high- or low-ranking animals endure more stress in a dominance hierarchy [6]. Ultimately, the reason why a psychosocial stressor is experienced as such by a given individual may depend on the amount of control exerted over its termination and the predictability of its occurence.

In humans, absolute dominance ranks have little meaning because of the multidimensional nature of social success in our species. It has been found that low socioeconomic status (SES) is reliably associated with a disruption of endogenous circadian fluctuations in cortisol levels, suggesting that cortisol might be linked with social hierarchy in our species as well [78,79]. The influence of parental SES and parent education in this phenomenon [80] may suggest the existence of a transgenerational epigenetic mechanism as observed in stress-related disorders [81], as the relationship holds after controlling for many confounding factors including the offspring's actual SES. This finding is also consistent with the well-established observation that uncontrollable psychosocial stressors involving a real or possible social subordination component invariably induce stress and cortisol release in humans [82,83].

The exact cognitive role of testosterone in humans is still debated. Although early studies proposed that testosterone plays a role in reactive aggression rather than aggression per se, studies proposed that it has an important function to establish social status in both men and women [71,84]. Yet, testosterone does not

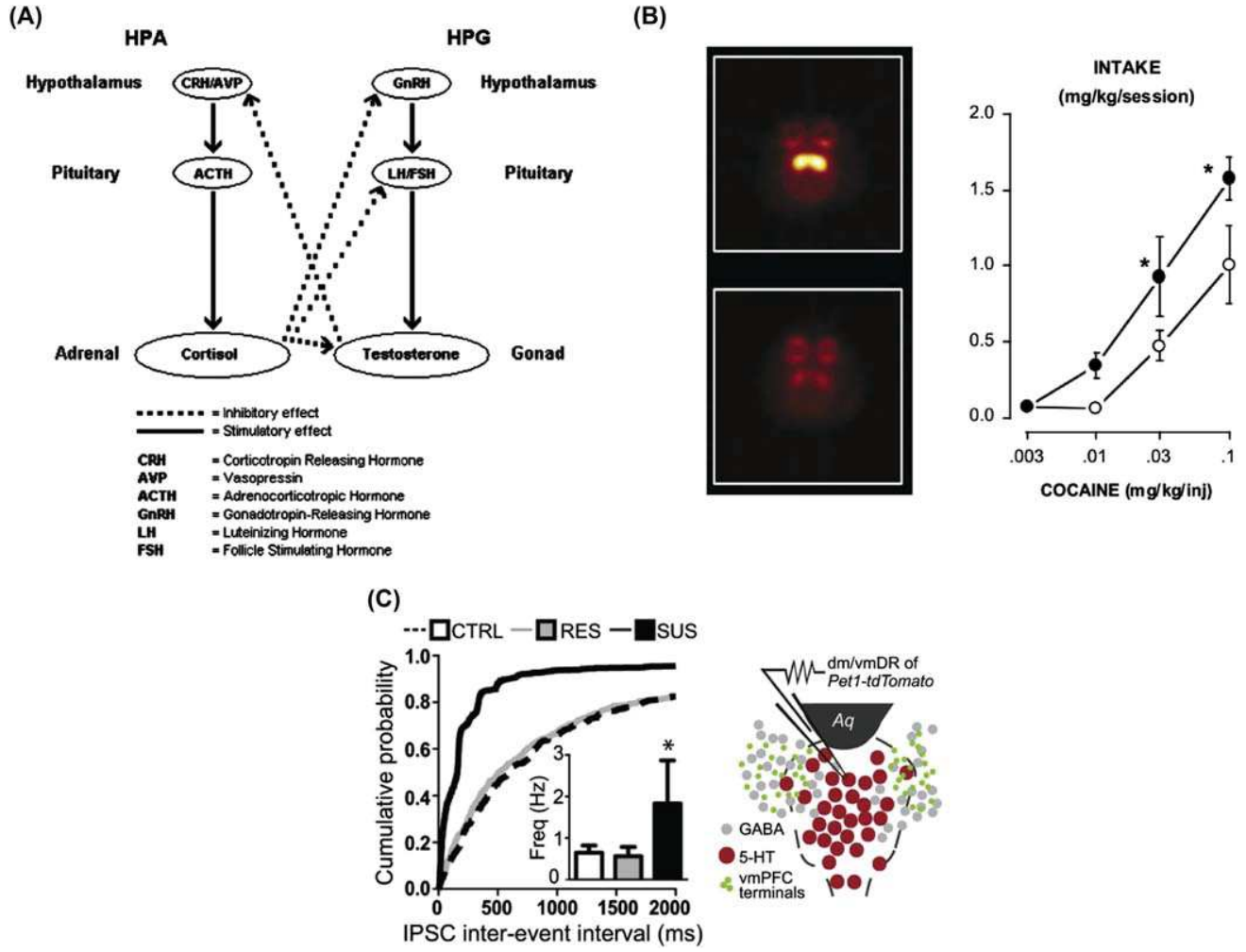

FIGURE 17.4 **Hormonal and neuromodulatory bases of social dominance**. (A) **Complexities of the cortisol–testosterone relationship involved in the maintenance of social dominance**. The hypothalamic–pituitary–adrenal (*HPA*) and hypothalamic–pituitary–gonadal (*HPG*) axes are represented with the brain structures involved, hormonal cascades, and functional interrelations. *(From Terburg D et al. The testosterone-cortisol ratio: a hormonal marker for proneness to social aggression. Int J L Psychiatry 2009;32:216–23, with permission.)* (B) **Role of dopamine in the emergence of social dominance and facilitation of cocaine addiction in subordinate individuals**. [^{18}F]FCP binding potential increases in dominant monkeys (*left*). (*Right*) Mean intake of cocaine per session for dominant (*white symbols*) and subordinate (*black symbols*) monkeys, as a function of the cocaine concentration in the self-administered solution. *(From Morgan D et al. Social dominance in monkeys: dopamine D2 receptors and cocaine self-administration. Nat Neurosci 2002:169–74.)* (*FCP,* fluoroclebopride) (C) **Involvement of serotonin neurons in the behavioral consequences of social defeats**. Optogenetic targeting showed that the serotonin neurons of susceptible (*SUS*) mice showing anxiety-like symptoms following social defeats were more inhibited than control (*CTRL*) or resilient (*RES*) mice showing no such symptoms. *5-HT*, serotonin; *vmPFC*, ventromedial prefrontal cortex. (*dm/vmDR*, dorsomedial/ventromedial dorsal raphe; *IPSC*, inhibitory post synaptic potential) *(From Challis C, et al. Raphe GABAergic neurons mediate the acquisition of avoidance after social defeat. J Neurosci 2013;33:13978–88. 13988a, with permission.)*

correlate linearly with socioeconomic status in humans, for two reasons. First, the aggressive tendencies of high-testosterone individuals are generally counterselected in many social organizations. Second, the net behavioral effects of testosterone on dominance-related behaviors depend upon cortisol levels: indeed, when resting cortisol levels are high, the positive association seen between dominance behaviors and testosterone is lost or even reversed [10,84]. A plausible role for testosterone would thus be to regulate the salience of and the reactivity to social threats as a function of dominance ranks [85], whereas glucocorticoids would modulate the ability to shift flexibly between a "salience" network, which supports rapid but rigid decisions, and an "executive control" network, which supports flexible, elaborate social decisions (see also Chapter 30). According to this hypothesis, one may expect that the high and disruptive cortisol levels observed in chronic stress diminish the social and biological value of testosterone-mediated dominance behaviors because of

the loss in behavioral flexibility. Moreover, transient fluctuations in cortisol levels seem causally involved in the adaptive memorization of social dominance relationships induced by competitive encounters [86], hence implying that disruption of cortisol signaling leads to imprecise representations of social dominance relationships.

While the HPG and HPA axes certainly play an important role in the implementation of proximal dominance behaviors, such as the arbitration of the "flee–fight–think" dilemma elicited by any social conflict, their functional physiology seems incompatible with the implementation of higher-order cognitive processes modulated by learned social hierarchies. The phenomena reported above are more likely to be mediated by central dopaminergic and serotonergic systems. Indeed, their modes of release in the forebrain enable also a refined coding of social information. To date, only a limited literature has investigated their roles in the social hierarchies of humans and nonhumans because of the methodological constraints associated with the measurement of central neuromodulators.

Dopamine, Serotonin, and Social Hierarchies in Rodents and Nonhuman Primates

In rodents, the emergence of an avoidant, subordinate behavior following social defeat is causally mediated by plasticity in the ventral tegmental area (VTA; containing dopamine neurons) occurring during and after a competitive interaction with negative outcome. More precisely, the sensitization of dopamine (DA) neurons occurs only in "susceptible" mice, which display a subordinate behavioral pattern following social defeats [87], and transient light stimulation of the VTA 1 day after social competition can reinstate avoidance and anhedonia symptoms induced by social defeats in most mice (Chaudhury et al. [88]). Suppression of dopaminergic firing may thus doubly contribute to the emergence of submissive behavior by inhibiting reward-related processes and by exacerbating the avoidance of subsequent social contacts with others, especially when they are dominant.

An outstanding question is whether postsynaptic sites to dopaminergic neurons are modulated by DA during social interaction. Does DA encode the presence/absence of dominant individuals? Does it encode social prediction errors (see "Social Hierarchies as a Major Evolutionary Pressure and Pivotal Feature of Societies") as in nonsocial settings? In dominant rats, microdialysis experiments showed that the imminence of a social conflict induces a strong release of DA in the nucleus accumbens [89,90]. In monkeys, no study has investigated dopaminergic firing per se as of this writing, but the perception of dominant individuals was shown to interfere with a reward valuation process typically controlled by DA neurons [91,92], and one study showed that neurons in the ventral striatum—intensely innervated by DA neurons—may encode the experience of social subordination and dominance during social conflicts over reward [93]. These findings are highly relevant for clinicians, because the emergence of dominance hierarchies within groups of monkeys induced reversible changes in D2/D3 receptor availability, which mediates detrimental behavioral changes in subordinate individuals, including enhanced susceptibility to cocaine addiction (Fig. 17.4B) [94,95]. Interestingly, a later study extended this finding to humans, using a subjective social status questionnaire [96]. Beyond the evidence they provide for an involvement of DA in learning social dominance relationships, these fluctuations of D2/D3 receptors may also explain why recreational dopaminergic drugs are able to artificially upregulate self-esteem, self-confidence, and social dominance in the short term; why they result in degenerate social behavior patterns when used for a longer term; and why the experience of juvenile social stress, dominance motives, and low SES predispose to psychostimulant usage [5,97].

Compared to DA, the exact roles played by serotonin in reinforcement learning are less clear and constitute an active area of research. Nonetheless, this neurotransmitter is undoubtedly involved in the adaptive regulation of many aspects of social and nonsocial behaviors [98]. An influential theory has long maintained that serotonin (5-HT) might implement the coupling between the anticipation of aversive events and behavioral inhibition [99,100], which strongly resonates with situations of social subordination in which one has to inhibit the decision to compete for resources in front of threatening and powerful conspecifics. An outsider theory—which recently gained strong empirical support from electrophysiological recordings and optogenetic manipulation of 5-HT neurons [101,102]—proposed that serotonin firing might instead promote patience and cognitive control within both appetitive and aversive contexts [103]. Interesting, this second theory also resonates with dominance relationships, as dominant individuals tend to be impulsive decision-makers, whereas subordinates typically have to "wait their turn," because of the core importance of pecking orders in any dominance hierarchy (for both nutritional and social resources).

To date, the most striking demonstration of the causal role played by serotonin in the establishment of social hierarchies comes perhaps from the study of Raleigh and collaborators [46]. In this series of experiments performed in 12 groups of three vervet monkeys, the authors showed that the "enhancement of serotonin signaling"

by a selective reuptake inhibitor and the suppression of serotonin signaling by a nonselective serotonin antagonist could induce dominance or subordination, respectively, in treated monkeys. More recently, it was confirmed that social defeats trigger sensitization of GABAergic neurons in the main serotonergic dorsal raphe nucleus (DRN) irrigating the forebrain [104]. Mirroring the aforementioned effect in the VTA [87,88], this sensitization phenomenon was visible only in the "susceptible" mice, which displayed an avoidant, subordinate-like behavioral pattern following social defeats (Fig. 17.4C). In humans, evidence supporting a role of 5-HT in social dominance is still sparse, but it was shown that enhancing 5-HT level through antidepressant medications or tryptophan supplementation (i.e., the precursor of 5-HT biosynthesis) might increase the frequency of dominance-related behaviors in everyday life [105,106]. Finally, in line with the definition of social dominance as an asymmetry of control over social stressors and social rewards, strong empirical evidence has emphasized that the reciprocal connections between the serotonergic DRN and the MPFC are crucial to adapt behavior in front of controllable stressors [87,107].

The joint involvement of DA and 5-HT in social dominance thus suggests (1) that the learning and decision-making processes controlled by these neuromodulators are central to the emergence of social hierarchies in mammals, (2) that social dominance might affect domain-general learning and decision-making through its influence on those neuromodulatory systems, and (3) that these neuromodulatory systems might have been sculpted throughout evolution to facilitate high flexibility in social behaviors, as required in species forming a dominance hierarchy. However, more research is needed to elucidate their exact computational roles, because no study has investigated how DA and 5-HT neurons react to conspecifics of different social ranks nor how they would implement the decision to compete or not against others.

CONCLUSION

The study of social dominance promises much more than simply accounting for interindividual differences in behavior and neurophysiology. Indeed, social dominance processes may offer mechanistic explanations for the emergence of such differences. Animal research indicates that social dominance affects serotonergic and dopaminergic neuromodulatory pathways responsible for behavioral and neural plasticity. It also affects the anatomical and functional properties of several brain structures traditionally linked with social and nonsocial perception, learning, and decision-making. It is the very nature of dominance hierarchies to shape social behaviors and to promote the coexistence of various profiles within a single social group. In this perspective, the development of refined computational models and social learning tasks probing social dominance in humans (coupled with neuroimaging) may help us understand and treat specific psychosocial disorders that seem particularly prevalent in humans relative to other apes, such as pathological aggression, social anxiety, schizophrenia, psychopathy, and some forms of depression.

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