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# Brain representations of social hierarchy

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## Executive Summary

- Social dominance refers to relationships wherein the goals of one individual prevail over the goals of another individual in a systematic manner.
- Dominance hierarchies are key evolutionary forces driving dyadic asymmetries in a group.
- Understanding how the brain detects, represents and monitors social dominance hierarchies constitutes a fundamental topic for social neuroscience.
- Representations of dominance hierarchies emerge early in development of infants and children.
- Distinct brain networks are engaged in representing social dominance from visual cues (eg. faces, body postures, viewing social interactions), when learning social ranks by observation, and through direct dyadic competitive social interactions.
- Learning social hierarchy information engages the anterior medial prefrontal cortex, 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 functional MRI.
- Dominance relationships are learned incrementally, by accumulating positive and negative competitive feedbacks associated to specific individuals and others members of the social group.
- The emergence of social dominance can be considered as a reinforcement learning problem inspired by neurocomputational approaches traditionally applied to non-social cognition.
- This research has implications for bullying prevention programs in children and adolescents, and can help to understand the neural mechanisms underlying imbalance of power between individuals.

### Introduction

Navigating the social world requires an accurate understanding of interpersonal relationships and their outcomes. An important factor that structures social life is *hierarchy*. This notion characterizes the fact that, in a dyadic relationship, one individual can be in an advantageous position with respect to another: S/he may exert power over another, monopolize access to a resources or enjoy a greater prestige. The emergence and development of the ability to evaluate and learn social hierarchy signals at early ages is an important topic for developmental psychology and social/cognitive neuroscience. Recognizing who is dominant and subordinate, predicting how an individual will behave according to his hierarchical rank, and knowing who is entitled to which resources as a function of rank are crucial cognitive capacities for knowing one's own place in a group.

Social dominance relationships can be defined as situations in which an individual controls or dictates others' behavior, primarily in competitive situations. Social dominance asymmetries constitute an important aspect, required to understand social organizations, and to predict how others will behave. Understanding how individuals evaluate, justify or act against dominance based-inequalities is also important to develop strategies to reduce inequalities and bullying behavior. The latter can be defined as repeated acts of aggression, intimidation, or coercion against a victim who is weaker in terms of physical size, psychological/social power, or other factors that result in a notable power differential. Such understanding has also the potential to increase cooperation, social harmony and educational performance.

### Developmental research on social dominance hierarchies

Recent research from developmental psychology indicates that preschoolers and infants can represent dominance relationships between social agents by exploiting a number of dominance-related cues, such as body size, to predict the outcomes of conflicts between social agents (Brey & Shutts, 2015; Charafeddine et al., 2016; Gülgöz & Gelman, 2017; Mascaro & Csibra, 2012; Over & Carpenter, 2015; Thomsen et al., 2011). There is evidence that distinct strategies can be used to attain higher social rank, such as power through the use of force and intimidation to induce fear, or prestige, through the sharing of expertise to gain respect (Cheng et al., 2013). Ten-month-old infants are already sensitive to dominance relationships. They expect an agent with a larger body size to prevail over a smaller agent (Thomsen et al., 2011). Fifteen-month-old infants also use conflicts over resources to predict social asymmetry (Mascaro & Csibra, 2012, 2014). That is, they expect an agent that has prevailed over another in a previous conflict, involving one type of resource (e.g. territorial resources), to also prevail in a conflict involving another type of resource. Another study found that 21- to 31-month-old toddlers preferred the winning character of a social interaction, in which one of two characters prevailed over the other (Thomas et al., 2018). However, when the winning character used coercive force, toddlers preferred the losing character, suggesting that they dislike the antisocial behavior of the former.

Preschoolers exhibit sophisticated ability to understand dominance (Brey & Shutts, 2015; Charafeddine et al., 2016; Gülgöz & Gelman, 2017; Over & Carpenter, 2015). At three years of age, they infer dominance from a variety of cues: the dominant is the one who shows physical supremacy over another individual, who is older, who imposes his choice or who has more resources. Preschoolers also use dominance relationships to infer various attributes of the dominant and subordinate individuals, such as the quantity of resources one owns or competence. One study reported that preschool children prefer higher status characters (eg. physical dominance, decision power, prestige, and wealth) (Enright et al., 2020). In contrast, another study reported that only 3-year-old children, but not 4- and 5-year-olds, preferred characters who imposed their choice (Charafeddine et al., 2018). Other studies did not show clear preference (Bernard et al., 2016; Castelain et al., 2016; Charafeddine et al., 2016; Enright et al., 2020). To predict dominance, older children also use the faces and body postures of social agents, as well as information about their wealth or age (Brey & Shutts, 2015; Charafeddine et al., 2015). Recent studies have reported that preschoolers can make explicit judgments of dominance through the observation of a wide variety of non-agonistic 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 (Charafeddine et al., 2015; Gülgöz & Gelman, 2017). Developmental psychology studies indicate that sensitivity to more elaborate dimensions of hierarchy emerges at a later stage. For example, five-year-olds, but not younger children, consider that being imitated and setting norms for others are signs of a powerful position (Gülgöz & Gelman, 2017; Over & Carpenter, 2015).

Another related topic of research has investigated how children allocate resources according to power. Since dominant individuals are more successful in their groups, they might be perceived as more competent and more knowledgeable. Two studies showed that preschoolers follow such heuristics (Bernard et al., 2016; Castelain et al., 2016). 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, there is a tendency to counteract inequity with age. That is, older children are more likely to give a greater amount of resources to a low-power character than to a high-power character (Charafeddine et al., 2016; Enright et al., 2020).

## Neural bases of dominance features from visual cues

Current knowledge about the brain representation of social hierarchy comes from neuroimaging studies in healthy adults. A number of early fMRI studies investigated the perception of social ranks based on visual cues, such as explicit representation of ranks (Zink et al., 2008b), postures (Marsh et al., 2009; Mason et al., 2014), uniforms (Chiao et al., 2009), facial traits (Todorov & Engell, 2008), as well as intelligence, celebrity or height (Farrow et al., 2011; Lindner et al., 2008). These early studies revealed an attentional network, that includes the lateral prefrontal cortex (PFC) and the intraparietal sulcus region, responds to dominance cues and is engaged during rank perception in a broad set of tasks (**Figure 1,** yellow).

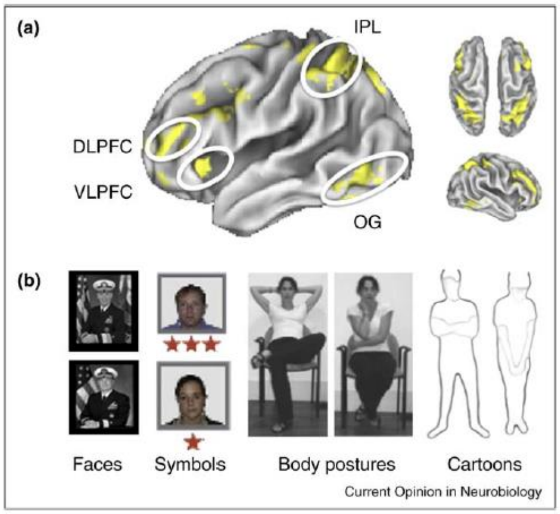


**Figure 1.** (a) Brain regions typically associated in recognizing social status of others. IPL, inferior parietal lobe; DLPFC, dorsolateral prefrontal cortex; VLPFC, ventrolateral prefrontal cortex; and OG, occipitotemporal gyrus. (b) Example stimulus material from neuroimaging studies of social status hierarchy, including facial postures, symbols, body postures and cartoons. Adapted from Chiao et al. (2010). Copyright Current Opinion in Neurobiology.

Faces are one of the most relevant categories of visual stimuli in our social environment, and face processing has been widely studied in neuroscience since many years. Facial features are central in predicting the social abilities and traits of others, and inferences of competence from faces even predict election outcomes (Todorov et al., 2005). A classical study showed that the variance in our social judgments from faces can be reduced to two main dimensions: trustworthiness and dominance (Oosterhof & Todorov, 2008) (**Figure 2**). Assessing features from a face is an important mechanism because such judgments predict significant social outcomes in domains as diverse as politics, business and mate choice (Lee & Seo, 2016; Ligneul et al., 2017; Sliwa & Freiwald, 2017). For example, in the domain of politics, candidates' chances of electoral success are related to whether their faces make them look competent, dominant, sociable, threatening or conservative (Oosterhof & Todorov, 2008). Moreover, forming rapid impressions from faces appears early during development. Indeed, leadership attributions made by young children closely match those made by adults when looking at the same faces. A substantial number of neuroimaging studies have used computer-generated faces to investigate the neural mechanisms which underlie judgements of people from their facial traits. While these studies have revealed that the amygdala tracks perceived trustworthiness, the dominance dimension has yielded several negative results (Chiao et al., 2009; Suzuki et al., 2015). Dominance feature from faces have also been investigated using facial physical features such the facial Width-to-Height Ratio (fWHR), which corresponds to the perceived rectangle formed from the distance between the eyebrow and upper lip extrapolated across the width of the face. A larger fWHR provokes an increased perception of social dominance in adults (Carré et al., 2009, 2010; Carré & McCormick, 2008; Lefevre & Lewis, 2013; Stirrat & Perrett, 2012), which could lead to avoidance behavior. Further neuroimaging work needs to be done in children and adults to determine how dominance in faces is represented in the brain. In children, it is likely that the same brain networks represent social hierarchies, but this remains to be investigated. Potential candidates include the intraparietal sulcus region, known to be engaged in rank comparisons in adults (Chiao, 2010) because it is involved in number comparisons and transitive reasoning in both adults and children (Cantlon et al., 2006; Farrow et al., 2011; Izard et al., 2008; Prado et al., 2010) (**Figure 1**).

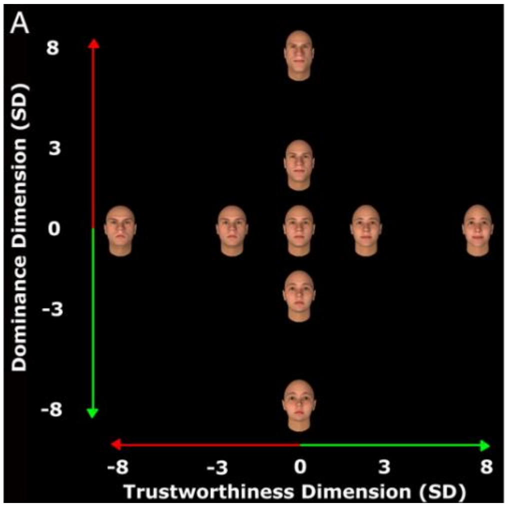


**Figure 2.** A model of face evaluation (Oosterhof and Todorov, 2008). Examples of a computerized faces varying on the two orthogonal dimensions, trustworthiness and dominance. The face changes were implemented in a computer model based on trustworthiness and dominance judgments of emotionally neutral faces. Copyright PNAS.

## Brain systems engaged in learning social hierarchy

One limitation of the neuroimaging studies investigating the brain representations of social hierarchy from visual cues is that many of the brain regions engaged may be related to general attentional, emotional and inferential processes associated with hierarchy processing rather than to the neural representation of hierarchy *per se*. In addition to these neuroimaging investigations on the perception of social ranks, recent studies have combined fMRI with computational modelling to address how the brain learns social ranks, either by observation or through competitive dyadic interactions (Kumaran et al., 2016; Ligneul et al., 2016; Wittmann et al., 2016). These latter model-based fMRI studies allow us to identify the neurocomputational mechanisms at play when learning social hierarchies by characterizing the computational processes identified by modeling behavior and by elucidating where in the brain they are implemented (rather than performing simple brain mapping methods comparing between two conditions A and B).

In the first type of situation, individuals monitor social interactions by observing others, this allows them to infer dominance relationships. Thus they may avoid competition against dominant individuals and to seek alliances with them. In one study, participants had to learn social ranks of a linear hierarchy. They were presented with two faces on a screen at a time and had to select which of them they thought had more power, which was followed by a feedback (i.e. correct vs incorrect). Participants acquired and represented transitive ranking relationships. The medial PFC (mPFC), and more specifically the anterior cingulate gyrus (ACCg) were engaged in learning ranks, computing estimates of individuals' power within a hierarchy, and updating knowledge about one's own hierarchy (Kumaran et al., 2016). Moreover, neural activity in the amygdala and anterior hippocampus tracked the emergence of knowledge about social hierarchies, with the hippocampus being also involved in the representation of non-social hierarchies (Kumaran et al., 2012).

In the second type of situation (i.e learning through competitive interactions), dominance relationships are learned incrementally, by accumulating positive and negative competitive feedbacks associated with specific individuals. A competitive outcome thus provides information about others' performances – which underlie the representation of objective social hierarchies – and information about oneself. During agonistic interactions, monitoring the probability of winning *vs* losing enables the individual to decide whether they should carry on fighting, or disengage from the confrontation in order to limit the physical and social costs associated with a defeat.

Outside agonistic interactions, monitoring such probability prevents the escalation of social conflicts for which the risks of losing outweigh expected benefits. In the cost-benefit trade-off, which underlies the decision to compete against another conspecific, the *cost* is typically associated with a property of the opponent (i.e., his strength or skill, which translate into a given probability of losing and a given effort to be exerted when trying to win). The *benefit* usually depends on the external resource which is at stake, (a notable exception being social competitive *play* in which no such external incentive is present). A recent fMRI study induced an implicit dominance hierarchy in men through a competitive game involving three opponents of different strengths (Ligneul et al., 2016). The rostromedial cortex tracked the dominance status of opponents, and also encoded opponent-specific prediction errors (**Figure 3**). Electrical stimulation of the rmPFC modulated learning and updating of social dominance representations (Ligneul et al., 2016; Qu et al., 2017; Qu & Dreher, 2018). These findings demonstrate a key role of rmPFC computations in dominance learning and unravel a fundamental mechanism that governs the emergence and maintenance of social dominance relationships in humans (**Figure 3**).

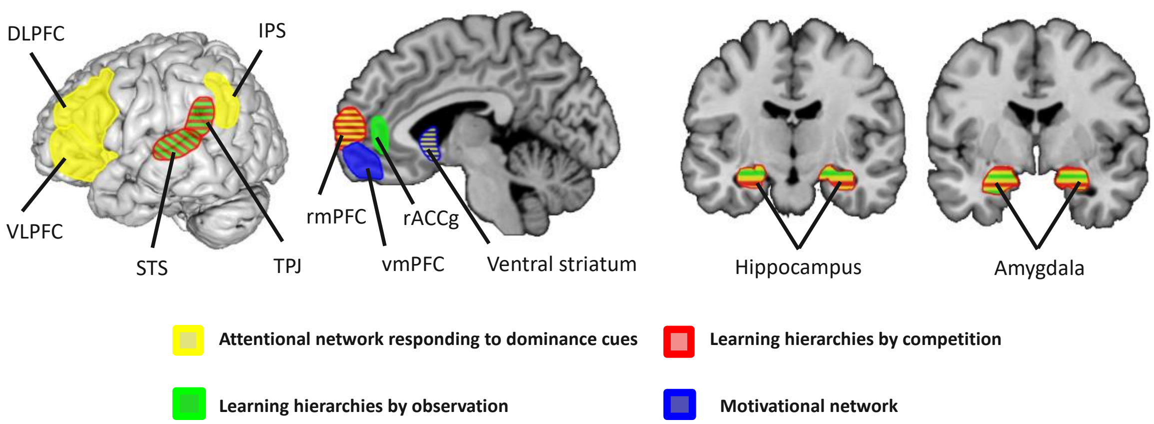


**Figure 3.** Main Brain Networks Engaged in encoding social dominance relationships. These networks include representation of social hierarchies based on the perception of social ranks from visual cues (yellow), when learning social hierarchies by observation (green), when learning by direct dyadic 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, which recruits the rmPFC, 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. 

These brain networks engaged in learning social ranks complement classical neuroimaging studies that indicate a motivational network, also known as the Brain Valuation System (BVS), composed of the vmPFC and the ventral striatum, is engaged in learning by reinforcement when the consequence of one's action is compared with a corrective feedback (**Figure 3**, blue). In particular, the ventral striatum is more engaged by social victories than defeats, which is thought to derive from prediction error signal, providing a key learning signal by reflecting the discrepancy between one's expectation and the outcome effectively obtained (reward vs punishment ) (Bos et al., 2013; Fareri & Delgado, 2013; Katsyri et al., 2012; Le Bouc & Pessiglione, 2013; Zink et al., 2008a).

## From learning social ranks to the ability to make transitive inferences

Knowing the ranks of other individuals may serve to make inferences about them and about the social structure of their group. When dominance structures are linear and transitive, i.e. if A dominates B and B dominates C, then A will likely dominate C, knowing who is dominant between A and C can thus be achieved through transitive inference. Early developmental approaches viewed transitive reasoning as a domain-general ability that could hardly be acquired before 4 years of age (Wright, 2001). However, recent studies using paradigms based on the presentation of dominance interactions showed that 10–15-month-old infants can actually make such transitive inferences (Gazes et al., 2017; Mascaro & Csibra, 2012). 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 (Charafeddine et al., 2015). 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 (Enright et al., 2017).

The neural bases of making transitive inferences after learning a hierarchy have been identified. In a recent fMRI experiment performed in adults, after learning a social hierarchy, participants viewed non-adjacent faces in the hierarchy (i.e. never seen together) and had to infer the higher ranking face while no feedback was provided (Kumaran et al., 2016). The bilateral amygdala, vmPFC and bilateral anterior hippocampus showed a significant correlation with absolute difference between individuals' power. These findings provide evidence that the anterior hippocampus and amygdala play a specific role in social rank judgments.

## Rank aversion reversal and social dominance orientation

Humans are known to be averse to inequality and this has been demonstrated using a number of behavioral economics games. However, people sometimes support inequality to avoid reversing the rank of others in society. In a behavioral economics redistribution game, people have been shown to choose more unequal outcomes to preserve existing hierarchies (Xie et al., 2017). When a proposed transfer reversed pre-existing income rankings, adults across cultures were twice as likely to reject the transfer. This human aversion to reversing rank is observed at an early age and across cultures. Inequality aversion develops between the ages of four and five, and rank reversal aversion develops between the ages of six and seven. The preservation of stable hierarchies observed in humans and animals has been proposed to be rooted in the willingness to reduce in-group violence and conflict. Although inequity aversion is often associated with higher engagement of the anterior insula and the anterior cingulate cortex (Sanfey et al., 2003), the neural bases of rank reversal aversion remain to be determined.

Finally, it is important to note that we are not all equal towards perception of social hierarchy. One key measure of interindividual difference between those who legitimize existing dominance hierarchies and those who condemn them when confronting socioeconomic inequalities is determined by a scale called the social dominance orientation scale (SDO) (Pratto et al., 1994). SDO is a general attitudinal orientation toward intergroup relations, reflecting preference for such relations to be hierarchical vs equal. High SDO reflects values of power, dominance and superiority over others (i.e. favoring inequalities in the access to resources). This is also associated with political attitudes supporting dominance hierarchies. A recent study suggests that differences between low and high SDO individuals may stem from variations in the brain sensitivity to dominance ranks, which may underpin this ideological split in the legitimization of dominance hierarchies (Ligneul et al., 2017). Following a competitive task used to induce dominance representations about three opponents (superior, equal and inferior), adults passively viewed the faces of these opponents while undergoing fMRI(Ligneul et al., 2017). Two key brain regions, the superior temporal sulcus (STS) and anterior dorsolateral prefrontal cortex (aDLPFC) were sensitive to social ranks, being more engaged with the SDO scale. That is, humans who legitimize dominance hierarchies and who believe that they derive naturally from asymmetries of ability show higher aDLPFC sensitivity to others' skills, and more particularly to those of dominant others. This finding suggests a link between the function of the aDLPFC and the psychological traits that mediate political attitudes regarding dominance hierarchies. The developmental roots at the origin of this personality trait remain to be investigated.

## Conclusions and Implications for education

One key question to address is how to translate developmental psychology and social neuroscience knowledge about the brain representations of social hierarchy to the classroom and education. We believe that decomposing the different neural processes engaged in the formation of social dominance hierarchies is a promising avenue that should offer mechanistic explanations for the emergence of interindividual differences in the perception and attitudes towards social dominance hierarchies. Here we have shown that it is possible to go beyond a descriptive approach. The neurocomputational mechanisms engaged when humans learn social ranks by observation or by direct competition are only beginning to be investigated, and this is a fruitful research direction that could stimulate different domains ranging from developmental psychology to social neuroscience. Ultimately, the study of the brain processes underlying our ability to track dominance relationships should pave the way towards innovative proposals for educators and policymakers to foster the reduction of inequality and asymmetry in power. Reducing inequalities helps to increases cooperation, social harmony and educational performance.

Current bullying prevention programs could also benefit from basic neuroscience knowledge reported here. A person is bullied when he or she is exposed, repeatedly and over time, to negative actions on the part of one or more other persons, and he or she has difficulty defending themself. This definition includes three important components: (a) aggressive behavior that involves unwanted, negative actions, (b) a pattern of behavior repeated over time, (c) an imbalance of power or strength. One reason why people bully may be to gain status in one domain when they cannot have it in another (e.g. academic achievement). Some of the current anti-bullying programs include simulations to help students think about how they can intervene to reduce bullying, as opposed to being a passive bystander. The neurocomputational mechanisms underlying such bystander effect have recently being identified in adults (Park et al., 2019), and anti-bullying programs could also benefit from these findings. These programs could benefit from understanding how the brain detects and learns social dominance hierarchies and acts against dominance based-inequalities. Research about the way the brain evaluates dominance may also help define the brain mechanisms involved and the age when intervention and prevention programs against bullying might be the most effective. For example, the fact 2-3 years old toddlers prefer those who win a social interaction, unless they use force to win (Thomas et al., 2018) suggest that there is an ideal age at which to start anti-bully programs.

Finally, another question would be to relate neuroscience research on social hierarchy and research addressing how socioeconomic status (SES) manifests in the brain (Farah, 2017). For example, children with low SES are more susceptible to learning deficits and lower academic achievement. At the brain system level, there are associations between brain structures and SES, such as brain volumes vary with neighborhood SES in adults, cortical thickness varies with income in children, and cortical surface area varies with parental education in children (Farah, 2017). Further work is needed to integrate these two domains of research.

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