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## Review

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## Keywords

Social hierarchies, perception, neurobiology, review.

### Palabras clave

Jerarquías sociales, percepción, neurobiología, revisión.

# Neurobiology of the perception of social hierarchies: current revision of the literature

Neurobiología de la percepción de las jerarquías sociales: revision actual de la literatura

## Abstract

Social hierarchies and their perception are a mechanism of fundamental social organization in many animal species, including human, which has a profound impact on aspects such as survival, social and reproductive behavior and health. Social dominance implies, among other things, the control of some individuals over the other members of the group, as well as greater access to resources. Considering that, from the evolutionary point of view, the social development and the cognitive and emotional processes related to this function are closely related to the development of the brain, the objective of the present review is to describe the neurobiological mechanisms involved in the perception of the hierarchy social, emphasizing the main experimental findings reported.

## Resumen

Las jerarquías sociales y su percepción son un mecanismo de organización social fundamental en muchas especies de animales, entre las que se incluye el humano, lo cual tiene un profundo impacto en aspectos como la supervivencia, la conducta social y reproductiva y la salud. La dominancia social implica, entre otras cosas, el control de algunos individuos sobre los otros miembros del grupo, así como un mayor acceso a los recursos. Considerando que, desde el punto de vista evolutivo, el desarrollo social y los procesos cognitivos y emocionales relacionados a esta función están estrechamente vinculados con el desarrollo del cerebro, el objetivo de la presente revisión es describir los mecanismos neurobiológicos implicados en la percepción de la jerarquización social, enfatizando los principales hallazgos experimentales reportados.

## Introduction

Social hierarchy and the perception of it underlies social relations between groups and is an important part of the social structure.<sup>1</sup> This has been observed in different species of animals in both simple and complex organisms.<sup>2</sup> Perceiving rank in a social domain is fundamental for an individual's welfare, even for their survival. The term social dominance is defined as a personality trait which involves a motive to control others, the self-perception of oneself as controlling others, and/or a behavioral outcome resulting from these motives or perceptions.<sup>3</sup>

In functional terms, dominion means that certain individuals have priority access to resources in competitive situations.<sup>4</sup>

In the socio-economic and socio-political human systems, the instances of domination hierarchies are established as monopolies, monarchies, social stratification, caste and class systems, sexism and racism, even in everyday human relationships between parents and children, spouses, siblings, colleagues, and friends, creating conflicts of disharmony.<sup>5</sup>

The determination of hierarchies depends on several factors, from biological aspects to the perception of signals from members of the group. In this way, reaching the top of the social hierarchy depends on the strength of character or personality traits (including courage, perseverance, and motivational drive), as well as a prior history of victory. Domain hierarchies produce marked inequalities in access to resources which can influence quality of life and health.<sup>6</sup>

This study aims to describe the neurobiological mechanisms involved in the perception of social hierarchies through the analysis of studies focused on this topic.

# The relationship between the brain and social behavior

Social dominance has been examined from different areas, including the recent studies focused on the role of the brain, highlighting the close dependence between the nature and type of social relationships and the anatomical and functional characteristics of different brain areas, even an underlying innate neural mechanism.<sup>5,7</sup>

Recent evidence shows that differences in brain structure correlate with the variation in the size of social networks of individuals.<sup>8</sup> From the Darwinian perspective, the evolution of intelligence is linked to life in social groups. The social brain hypothesis states that the development of social expertise was the key to the evolution of the primates' brain, as a function of coping with the complexities of such a social life.<sup>9</sup> In this sense, Darwin considered that the close relationship between the size of the brain and the development of the intellectual faculties in human beings is supported by comparing of the skulls of the wild races and the civilized races, skulls of the ancient and modern peoples and, by analogy, the whole series of vertebrates.<sup>10</sup> With respect to ontogenetic development, it is known that, from the first days of life, the human being has a physical mind, a social mind, and a linguistic mind, which enables him to respond effectively and adaptively to the demands in the respective domains.<sup>11</sup> Likewise, it has been observed that the perception of hierarchical dominance is already present in children as young as two years old.<sup>12</sup> Currently, it is

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known that brain development, brain activity, and behavior depend on inherited and environmental influences, and there is a growing appreciation that social information, in turn, can affect the expression and behavior of brain genes.<sup>13</sup>

# Genes, hormones, and neurotransmitters involved in social dominance

In humans and other primates, adverse social environments often translate into long-lasting physiological costs. The strong links between social status and risk of disease in humans suggest that such effects can be particularly accentuated in the primate immune system. The biological mechanisms associated with these effects are fundamental to understanding the evolutionary impacts of social behavior as in the context of human health. Currently, there are few studies aimed at studying how the social state affects gene regulation and the immunological and physiological aspects, especially at the molecular level. However, valuable information has been reported in this regard. For example, it is known that in environments in which hierarchies are strictly applied or subordinates have little social support, the low dominance range can lead to chronic stress, immune compromise, and reproductive dysregulation, with observed changes in the regulation of glucocorticoids, in sex steroid hormones, in serotonergic and dopaminergic signaling, and in the number and proliferation of lymphocytes.<sup>14</sup>

Genes. Several investigations aimed at studying the genomic and chemical mechanisms underlying social behavior have found that, although the challenges and social challenges facing animals are equivalent in all species, the answers are specific and that these behaviors are regulated by genetic modules and neurochemical codes. Geneenvironment interactions and social hierarchies identified in humans and non-human primates influence allelic variants that act by altering gene expression and regulation levels.<sup>15</sup> For example, one of the genes considered important in the molecular and cellular aspects of social behavior is *egr1*, and the different studies focused on this gene suggest that social experience could trigger changes in larger genetic networks involving many regions in the brain. Likewise, social signals can trigger lasting epigenetic modifications of the genome translated into hereditary changes in the expression of specific genes that are not due to changes in the DNA sequence. It has been found that, for example, in maternal behavior, methylation of the region promoting the glucocorticoid receptor gene of the stress hormone allows NGFI-A, the protein product of the *egr*1 gene, to regulate the expression of glucocorticoids, especially in the hippocampus.<sup>15</sup>

**Glucocorticoids.** Research conducted in captivity has reported that losing fights can increase glucocorticoid secretion as a general response to stress. Likewise, it has been argued that chronic stress could be the cause of the reproductive suppression of social subordinates. However, recent studies have also suggested that dominant individuals have higher glucocorticoid levels, which may suggest that not only dominated but also dominant individuals with high levels of glucocorticoid are at risk of impaired reproductive function.<sup>17</sup>

Sex steroids and neuropeptides. Both sex steroids and neuropeptide hormones have been implicitly modulated in all facets of social behavior, including aggression, sexual behavior, parental care, and sociability. On the one hand, sex steroids can affect neural circuits and behavior through genomic mechanisms that involve changes in gene expression, as well as through rapid effects mediated by cascades of signal transduction; on the other hand, neuropeptides exert their actions exclusively through peptides through cascades of signal transduction. It has been observed that hypothalamic peptides oxytocin and vasopressin mediate affiliative and sexual behaviors in several species of mammals. Serotonin is another neurotransmitter related to social behavior. especially social status and dominance in primates. Even selective inhibitors of serotonin reuptake influence social behavior in humans. Serotonin has also been linked to the modulation of aggressive social behavior. The endogenous opioids, in turn, modulate the circuits involved in social bonding, separation anxiety, and gambling.<sup>18</sup>

**Dopamine.** It has been shown that the chronic stress experienced by subordinate monkeys causes a down-regulation of the expression of dopamine D2 receptors.<sup>19</sup> Likewise, with the objective of stipulating predetermined or provoked aspects of the levels of dopamine D2 receptors in monkeys, it was found that the formation of a social hierarchy produced a gradient of dopamine D2 receptors.<sup>20</sup> In the same way, in another study conducted with humans it was reported that there is both the possibility that the serotonin and dopamine systems are modulated by the hierarchical position of an individual, as well as that the level of serotonin in blood also affects the social state of the individual.<sup>21</sup>

Lymphocytes. Chronic activation of the stress response by chronic psychosocial stressors (such as constant proximity to an anxiety-provoking member of the species) may increase the risk of numerous diseases or exacerbate preexisting conditions such as hypertension, atherosclerosis, insulin-resistant diabetes, immuno-suppression, reproductive alterations, and affective disorders. In particular, it has been observed how the stress caused by social dominance produces a profound suppression in the activity and proliferation of lymphocytes.<sup>22</sup> Likewise, it has been reported that social stress desensitizes lymphocytes to regulation by endogenous glucocorticoids, which undoubtedly has a detrimental impact on the physical health of those who suffer from it.23

#### Brain areas involved in social dominance

Some brain regions involved in the perception and learning of social dominance have been identified, which include: the amygdala, the hippocampus, the striatum, the intraparietal sulcus (IPS), the ventromedial prefrontal cortex (VMPFC), and the lateral prefrontal cortex (LPFC), which can be classified into two groups:<sup>24</sup>

I. A group that codes only the social classification and includes:

Lateral prefrontal cortex. This part of the cortex seems to be involved in the perception of social dominance. For example, greater activation of the dorsolateral prefrontal cortex (Brodmann areas 9 and 46) has been observed when participants perceive gestures or faces or images of people with a high rank or social hierarchy compared with those of low social rank.<sup>25,26</sup>

Likewise, the ventral lateral cortex (mainly Brodmann area 47) has exhibited a greater activation before specifically human social hierarchies.<sup>27</sup> The specificity of this brain region is unknown, but it is hypothesized that it could have a relationship with the attentional system based on evidence from previous studies. The great activation observed in the ventral lateral cortex during social interaction with socially dominant persons is very likely to reflect a great intensity of attention.<sup>28,29</sup>

The lateral prefrontal cortex also plays an important role in compliance with social norms.<sup>30</sup>

With respect to the functional differences of the lateral prefrontal cortex and the ventral lateral prefrontal cortex, it has been suggested that they participate in different cognitive demands;<sup>31</sup> however, this position is still unclear at present.

Amygdala. The role of the amygdala has been reported in different measures aimed at the study of social dominance, such as a) the detection of interpersonal distance,<sup>32</sup> b) the nature of a hierarchy (stable or unstable) or the context of a classification (social or not social),<sup>25</sup> c) during the inference of social classification.<sup>33,34</sup>

Anterior hippocampus. The anterior part of the hippocampus (which has connections with the amygdala) is related to the level of individual confidence with respect to the inference of social classifications.<sup>33</sup>

II. A group related to social dominance and that codifies social and non-social hierarchies and is formed by:

**Ventromedial prefrontal cortex.** Some studies have shown that this part of the cerebral cortex seems to have a specific role for the perception

of clues of dominance.<sup>26,35</sup> One study showed how patients with lesions in the ventromedial cortex are insensitive to specific perceptual cues of social hierarchical value such as age and gender.<sup>35</sup> Likewise, a correlation has been found between the activity of the ventromedial cortex and the social and non-social hierarchies.<sup>33</sup>

**Intraparietal sulcus.** The participation of the intraparietal sulcus in the attentional orientation related to the perception of dominance has been observed. It has also been observed there is participation of this brain area in processing information related to "rank" independently of content (social or non-social), as well as with the "magnitude."<sup>25,36,37</sup>

Striatum. Zink et al<sup>25</sup> found that seeing the face of a higher-ranking opponent causes a greater degree of activity in the ventral striatum than when seeing the face of a lower-ranked opponent. They also reported increased activation of the striatum when participants were informed of their victory or loss and when they defeated a superior human player. However, this activation did not occur when the participants defeated a superior computer player (non-social context). From another study, it was concluded that striatal activity can encode a social classification based on a biased sensitivity related to the participant's hierarchical status.<sup>38</sup>

Posterior hippocampus. It has been related to social and non-social classifications.<sup>33</sup>

# Brain circuits involved in social dominance

Currently, the neural circuit mechanism underlying social dominance is considered practically unknown.<sup>7</sup> The main systems and circuits in the vertebrates proposed by some authors are described next.

a) The mesolimbic reward system, whose main characteristic lies in its massive dopaminergic projections from the ventral tegmental area to the nucleus accumbens, and includes brain areas such as the lateral septum, the ventral pallidum, the striatum, the basolateral amygdala, the nucleus of the stria terminalis and the hippocampus.<sup>15</sup> Many studies indicate that through the mesolimbic reward system, the individual evaluates the relevance of the stimuli in order to generate an adaptive response.<sup>39,40</sup> Likewise, this system also mediates an individual's ability to adapt to chronic social stress.<sup>41</sup>

b) The so-called "social behavior network,"<sup>42</sup> which includes the lateral septum, the extended medial amygdala (i.e. medial amygdala and the bed nucleus of the stria terminalis), the preoptic area, the anterior hypothalamus, the ventromedial hypothalamus, and the periaqueductal gray matter.

All of these areas are reciprocally connected and express sex steroid receptors. The investigations carried out to date with respect to the functions of this network have evidenced their role in the mediation of sociability between species, as well as in paternal and maternal behavior.<sup>43,44</sup>

c) Circuit controlled by the prefrontal cortex. Some studies in which brain imaging technique was used in humans have reported the involvement of the dorsolateral and medial prefrontal cortex in social dominance behaviors.<sup>25,37</sup> The participation of this area underlies the cognitive functions that imply the recognition of the social condition, the learning of social norms, and the detection of the violation of the social norms involved in this function.<sup>5</sup> Likewise, with the objective of knowing where and how the information of social hierarchy in the brain is encoded, a study<sup>7</sup> was carried out through a paradigm of social dominance in mice and they found that there is a circuit controlled by the medial prefrontal cortex, in particular, the dorsal area, for the hierarchy of dominance. Through the projections of the medial prefrontal cortex to regions such as the dorsal raphe, the ventral tegmental area, the hypothalamus, and the amygdala, it exerts descending controls on the release of serotonin and dopamine, endocrine function and the response to fear which could contribute to the key characteristics

of domination behaviors, including aggression and the ability to respond to stress and fear. In particular, these researchers found that dominant mice have greater excitatory synaptic strength in the pyramidal neurons of the V layer than their subordinates, as well as a significantly greater number of positive c-Fos neurons in the prelimbic region of the medial prefrontal cortex.

### Neuroanatomical markers of the social hierarchy: studies with cerebral imaging and electroencephalogram

It has been reported that in several species, including humans, facial signals are used to express social dominance and submission, which are usually of two types: emotional expressions related to aggression and facial postures that vary in the look and in the vertical orientation of the head. The perception of dominance is related to facial expressions of anger, a sign of threat or possible aggression, a direct gaze, and an upward tilt of the head, while submission is conveyed with a fearful expression and facial postures with a fixed gaze and a downward tilt of the head.45,46,47 On the other hand, it has also been suggested that, in stable social hierarchies, the facial postures used by individuals are more neutral, regardless of dominance or submission.48

Considering the evolutionary importance of social dominance, it is interesting to know the cerebral mechanisms underlying the recognition of this function in humans; however, to this day, there are few studies carried out in this regard.

For example, a study was conducted through potential techniques related to events and functional magnetic resonance in which the neuronal mechanisms underlying the perception of social dominance from facial signals were examined.<sup>37</sup> They found that the perception of mastery of emotional expressions related to aggression occurs early in neuronal processing, while the perception of social dominance of facial postures emerges later. Brain imaging results show that the activity in the fusiform gyrus, superior temporal gyrus, and lingual gyrus, is associated

with the perception of social dominance of the facial postures and the magnitude of the neural response in these regions differentiates between the perceived dominance and the perceived submission. Likewise, another study was conducted with the objective of determining the neuroanatomical bases in the inference of the hierarchical identity<sup>49</sup> using the techniques of event-related potentials and structural magnetic resonance during the application of a computerized game in which the participants visually discriminated simulated players. One of these players performed successfully and, through different manipulations, often confirmed high status. Another simulated player presented an unsuccessful performance, exhibiting a lower rank. The participants showed a greater amplitude in the N170 component related to the perception of the image of a superior player compared to an inferior player, which was correlated with the cerebral morphology of the posterior cingulate cortex, the superior temporal gyrus, the insula, the fusiform gyrus, and the caudate nucleus.

On the other hand, with respect to the electroencephalographic technique, the perception and interpretation of social hierarchies has frequently been related to modulation in the alpha band<sup>50</sup> be it with the decrease and increase of this band in the right and left prefrontal cortex,<sup>51</sup> with a great reduction at the perception of faces that represent a high social rank,<sup>52</sup> or with an asymmetry correlated with self-reported dominance.<sup>53</sup>

# Conclusions

Although there are currently few studies focused on determining the neurobiological mechanisms involved in social hierarchy and its perception, the evolutionary relevance of this function in the social relationships of individuals is evident, even suggesting an underlying innate neural mechanism. The genes, hormones and neurotransmitters that modulate the perception of social dominance have been determined in some way, however, more studies are still needed to explore these topics. It is also necessary to expand the research focused on determining the cerebral areas underlying the social hierarchy, which, according to what has been reported so far, include the prefrontal, parietal, temporal cortex, the striatum, the hippocampus, the amygdala, as well as the reward circuit, the so-called social behavior network, and another circuit controlled by the prefrontal cortex. Undoubtedly, conducting research using techniques such as brain imaging, electroencephalogram, etc., will allow us to know more about the cerebral mechanisms related to this important social function.

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