CHAPTER

9

Neuroimaging Investigations of Social Status and Social Hierarchies

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OUTLINE

1. INTRODUCTION

Social hierarchies are omnipresent in the lives of many species. The ability to successfully navigate complex social environments with consideration of the relative rank of conspecifics is an essential skill not only for humans, but also for numerous other social beings. From maintaining rank and reducing conflict, to communication and reproduction, organisms of varying complexity rely on social hierarchies to support social interactions. Hierarchical social structures can provide order and clarify the roles of individual group members, thus facilitating social coordination. Furthermore, in some instances, status-based hierarchies can incentivize those lower in relative rank to progress and achieve higher standing among their peers, thus providing motivation to perform a variety of behaviors.

Social hierarchies have been identified across a broad range of organisms, from simpler model systems such as insects, to nonhuman and human primates. For example, reliance on status cues to organize important social behavior is identified in ants[1] and other insects, such as bees, who infer higher ranking in the social hierarchy based on physical body size.[2] Many species of fish are also known to rely on social hierarchies. For example, in *Cichlasoma dimerus* males (South American cichlid fish known to have stable and linear hierarchies), a greater social position within the hierarchy has been linked to lower relative stress levels and increased reproductive success.[3]

Neuroimaging Personality, Social Cognition, and Character
http://dx.doi.org/10.1016/B978-0-12-800935-2.00009-9

Greater complexity can be found in the social hierarchies of mammals, such as rats and primates, with increased research demonstrating the impact of relative social status on communication, reproductive behavior, and access to resources.[4,5] Among nonhuman primates, a diverse array of social structures and organizations support, sometimes simultaneously, the establishment and maintenance of social hierarchies. Positions within these more complex hierarchies often determine central aspects of their members' social interactions and life outcomes.[6–13] In line with the important benefits often associated with the possession of greater status (i.e., better health and reproductive success[14,15]), primates appear to value group members with greater social status. Whereas primates often find conspecifics rewarding compared to other stimuli,[16–19] research has found that macaques are willing to sacrifice primary rewards in order to see the faces of high-status others.[20] High-status primates often utilize overt displays of dominance, such as "chest-beating," to assert their position in the hierarchy; their status is often suggested to correlate with power, resource control, and preferential mate selection.[21–23] However, whereas such rigid status hierarchies may be prevalent among macaques and baboons, it appears not to be the case in other primate species such as the gibbon and howler monkey.[24,25]

Whereas the omnipresence of status-based hierarchical social organization among animals and humans alike is generally agreed upon, it is a challenge to provide a precise and inclusive definition of social status. When referring to humans, historians, sociologists, psychologists, and economists utilize a variety of generalizable definitions of social status. Perhaps one of the most common terms referring to human social status is socioeconomic status (SES). SES is a multidimensional construct usually based on objectively assessed factors related to education, occupation, and income.[26] Depending on the ages of the individuals, measures of SES will take into account their own education, occupation, and income but also those of their parents. Other measures of SES consider an individual's neighborhood of residence[27] or the subjective assessment of his or her perceived social standing relative to others.[28] Even if sizeable correlations between the factors comprising SES have been reported, it is important to note that distinct factors of SES, such as income and education, often reflect discrete past experiences and may often not be interchangeable or appropriately used as proxy variables for one another.[29,30] More fundamentally, a single and generalizable measure of social status is difficult to formulate when considering that social hierarchies can be based on various social dimensions and that the meaning of "being at the top" differs across individuals. For instance, some may perceive high status as referring to the possession of vast amounts of disposable income (i.e., high financial status), while others may place greater emphasis on physical characteristics, such as attractiveness or fitness, as symbols of high status. To others, high status may be conferred by prestigious occupations demonstrating intellectual accomplishments rather than financial wealth or by the enactment of prosocial behavior and the possession of well-developed moral principles.

Whereas research suggests that young children tend to ascribe higher status to individuals perceived to be more dominant,[31–33] adults base their judgments of others' social status on a wide range of socially valued dimensions that may or may not be perceptually available. For example, individuals believed to be immoral or bad tend to be assigned lower status.[34–37] Although what conveys social status may not always generalize across individuals and social groups, perceived differences in standing typically appear to be based on social dimensions valued by members of a given group.

Focusing henceforth solely on humans, the goal of the current chapter is to provide a review of recent insights into how differences in social status may impact brain structure and function. Although, considering the centrality of social status as a construct guiding social interactions, relatively little research has been done on the topic. Recent brain imaging investigations have begun to explore how our own social status shapes us and how the social status of others shapes our responses to them. In the subsequent sections, we will first begin by briefly examining available evidence of the influence of social status on brain structure and cognitive development. Subsequently, we will focus on recent functional Magnetic Resonance Imaging (fMRI) investigations on the impact of social status on how we construe others. Finally, we will present fMRI studies suggesting that individual differences in social status shape how we respond to others. Throughout the chapter, we also intend to highlight some of the behavioral data complementing these early brain imaging investigations of the impact that social hierarchies have on ourselves and on how we construe others.

2. SOCIAL STATUS AND BRAIN STRUCTURE: STATUS AS AN ENVIRONMENTAL FACTOR

Recent research indicates that social status, defined here as a social and environmental factor, has a sizeable impact on the development of neural structures and their functions. Advances in neuroimaging methodologies provides opportunities to investigate how various environmental factors associated with social status, particularly SES, impact brain functioning. In this section, we first review the somewhat disparate literature suggesting that different measures of SES may be associated with different structural brain differences. We will subsequently attempt to provide an overview of the growing body of literature exploring how differences in SES during development impact cognition and brain functions.

2.1 Measuring Social Status

As mentioned in the introduction of this chapter, social status is often measured in terms of one's socioeconomic status, or SES. Socioeconomic status typically refers to an individual's access to economic and social resources and is therefore considered a multidimensional construct.[26,29] As such, researchers investigating the link between SES and brain structure must make a number of careful decisions when defining SES. Research on SES often relies on a number of "proxies" to operationalize complex environmental factors. The most common factors selected by researchers to measure SES include income, educational attainment, occupational prestige, and information regarding an individual's neighborhood SES. In some circumstances, for instance, depending on the age of the individual, these factors may be assessed in terms of both the individual and his/her parents. Although many of these factors may be correlated, they should not be thought of as interchangeable since, for example, they may differentially impact developmental outcomes.[29]

2.2 Income

Income may be calculated using household, familial, or parental income in studies with child populations or solely by the income of the individual when studying adult populations.[30,38–45] While income has been used widely as a marker for SES, and therefore social status in general, in recent years it has fallen out of favor as a reliable measure due to the unreliability of self-report data from participants and the marked fluctuations of income over time at both an individual and familial level.[29] More recent studies have instead begun to use the Income-to-Needs (ITN) ratio. This ratio divides total family income by the official federal poverty threshold for a family of that size.[46] The ITN ratio now allows researchers to assess family income while also taking into account other important factors, such as national norms, family size, and cost of living, thereby providing a clearer measure of a family's financial standing.

2.3 Educational Attainment

Educational attainment, defined simply as the highest level of education completed by either the parents or the individual, is another component of SES that is often used to assess social status. Commonly used as a proxy for a number of factors related to cognitive stimulation in one's home environment, educational attainment is thought to measure the qualitative aspects of the relationship between the caregiver and child, such as exposure to complex language, parent–child interactions, and the quality of guardian caregiving practices.[47–53] The results of a number of studies focusing on maternal educational attainment, which is believed to be associated with better cognitive stimulation in the home environment, suggest that education may be the best predictor of a number of developmental outcomes.[54–56]

2.4 Additional Ways to Measure SES

Other ways of assessing SES include occupation (of either the parent(s) or the individual), average neighborhood SES, and subjective social status. Occupation is typically correlated with education and income, as particular occupations are normally associated with distinct levels of education and earnings.[57] Neighborhood SES, measured as the average SES of the individual's immediate neighborhood, is often found to be associated with exposure to environmental stressors, such as greater police presence, poverty, and higher prevalence of physical and social disorder, as well as limited access to institutional resources, such as libraries, medical care facilities, and overall employment opportunities.[27] Another measure commonly used by researchers is subjective social status: a self-report index that refers to an individual's perception of his or her own social rank relative to others within a defined group. Subjective social status is typically measured using the MacArthur Scale of Subjective Social Status. This scale requires individuals to indicate their place on a ten-rung ladder said to represent their larger community and has been found to predict a number of physical and mental health outcomes, above and beyond other, possibly more objective, measures of SES.[28,58]

Given the wide variety of measures used to define social status, many researchers prefer to use composite measures of SES, including a combination of two or more of the previously mentioned factors. Composite measures of SES commonly used in brain imaging research include the Hollingshead scale,[59] which combines occupation and education (Two-Factor Index), or education, occupation, marital status, and employment status (Four-Factor Index), as well as the Barratt Simplified Measure of Social Status,[60] which combines educational attainment, occupational prestige, and income.

2.5 Investigating the Impact of SES on Adult and Child Populations

Studies investigating the role of SES on brain development may choose to focus on adult populations, adolescents, or young children, each of which brings its own challenges. Since difficulties exist in assessing the SES of children and adolescents, studies examining these populations often rely on information from the child's guardian(s). Studies involving adult populations, however, can assess an individual's SES by taking into account the various measures discussed above. While this may provide a more accurate measure of current social standing, researchers do acknowledge that it may not accurately characterize the environmental and social factors that occurred during the individual's childhood (since biases in retroactive self-report data can affect the factors being assessed). In addition, researchers must also consider unforeseen circumstances that may cause changes in SES (in both adult and children), such as sudden unemployment or moving to a different neighborhood. In an attempt to address these issues, some researchers are conducting longitudinal studies following participants over the course of a given time period. Such studies allow researchers to examine the stability of an individual's status over time and the patterns of fluctuations in aspects of social status, which have been suggested to represent sources of stress.[45,61,62]

2.6 Challenges in the Study of SES and Brain Functions

Unfortunately, a number of challenges and difficulties face researchers investigating the role of SES on brain structure and development. As it may now be apparent, SES can be a difficult construct to define and measure; although SES has been shown to impact behavioral, educational, and life outcomes,[26,63–73] several studies have failed to establish a relationship between SES and brain function or structure.[41,42,44] Challenges arising when measuring brain morphometry, such as a lack of consensus on whether to measure brain volume or surface area of the cortex, are believed to contribute to these difficulties.[29] To further complicate matters, indices used to measure SES can be highly correlated with important mediators being considered, such as stress, nutrition, and family environment, making it difficult to isolate the effect of SES.[70,74] In spite of these various challenges, dedicated cognitive and developmental neuroscientists have begun to uncover how variations in social status lead to differences in neural structure and cognitive development.

2.7 Impact of SES on Brain and Cognitive Development

Typically demonstrating that low-SES individuals do not perform as well as their higher-SES counterparts, a number of studies found that SES is associated with the development of cognitive functions, such as language, executive function, memory, and visual cognition.[26,47,68,73–76] These findings tend to parallel results from behavioral studies, indicating that deprivation of resources (e.g., less cognitive stimulation from caregivers or home environments) leads to various impairments in cognitive performance.[47,77,78] In light of these findings, establishing how SES impacts the neural processes supporting these cognitive functions is believed to be a vital component of the development of interventions to improve the educational and life outcomes of lower SES individuals.

2.8 Executive Function

The term executive function is often used to describe cognitive processes involved in planning, execution, reasoning, and problem-solving.[79–82] Researchers often break down executive functions into a number of subprocesses often suggested to rely on prefrontal brain regions. Some examples of these subprocesses include working memory (the ability to hold information in the mind and use it to complete a task), inhibitory control (the ability to stop oneself from performing an action), and mental flexibility (the ability to sustain or flexibly switch between sets of behaviors, tasks, rules, or mental states).[79–82]

Decreased performance in executive function among lower-SES children has been reported in the literature. For example, using a delayed-response paradigm, in which infants had to search for an object hidden in one of two hiding places after a delay period, Lipina et al.[83] reported that low-SES infants made more errors when asked to inhibit an incorrect response and had worse memory for the spatial location of objects. In addition, low-SES infants had a greater rate of A-not-B errors—not correcting for the new hidden location of an object in a consecutive trial—which has been widely associated with an immaturity of object permanence.[84] Similarly, a study using a flanker task to assess cognitive operations related to alerting, orienting, and executive attention reported reduced speed and accuracy among low-SES children, indicating difficulty in inhibiting distracting information.[85]

Recent neuroimaging evidence suggests that brain regions associated with executive functions may develop differently for individuals with lower-SES backgrounds. In a study of children and adolescents aged 4–18 years old, Lawson et al.[43] reported that higher parental education predicts increased cortical thickness in the left superior frontal gyrus and right anterior cingulate gyrus, frontal brain areas linked to the ability to suppress or override competing responses while appropriately adjusting the effort required to do so.[86,87] These results are consistent with a study by Noble et al.[88] using diffusion tensor imaging (DTI) to investigate the structure of white matter in the brain of participants that varied on educational attainment. Their results suggest that lower educational attainment correlates with alteration of white matter tracts believed to be important for aspects of cognitive control when compared to participants with higher educational attainment.

Recent studies explored the potential relationship between gray matter volume and maternal occupation and education. In one such study, gray matter volume in a number of brain regions was found to be larger for children with mothers who have higher levels of educational attainment and greater job prestige (using the Hollingshead 2-factor index).[89] In another study, Raizada et al.[90] report a marginal association (possibly due to a low sample size) in five-year-old children between greater gray and white matter volumes, particularly in inferior frontal regions, and greater maternal education levels and occupational prestige. However, possibly the most convincing piece of evidence to support this relationship comes from a study by Noble et al.[91] investigating the relationship between SES and brain morphometry in a large sample of 1099 typically-developing individuals aged between 3 and 20 years. Results from this study also indicate a positive relationship between surface area in regions related to executive function and spatial skills and SES. Interestingly, the increase in surface area was found to be logarithmic, such that a subtle increase in income for lower-SES individuals is associated with a relatively large increase in surface area, suggesting that extremely disadvantaged children are the most negatively impacted.

Dysfunction in attention and executive function in low-SES children has also been demonstrated with the use of electrophysiology experiments. Using a technique measuring event-related potentials (ERPs), researchers have been able to investigate differences in attention allocation in children from different SES environments. ERPs allow researchers to measure electrical brain activity at the scalp and provide superior temporal resolution but poorer spatial resolution than fMRI. In one particular set of studies, where children were asked to listen to a story presented in one ear (the attended story) while ignoring a story playing in the other ear (unattended story), researchers found differences in the amplitude of the P1 component, a waveform associated with attention allocation occurring about 100 milliseconds following the presentation of the stimuli. Whereas higher-SES children displayed a greater P1 response corresponding to the hemisphere in which the attended story was presented, indicating correct discrimination of the distractor (or unattended) story playing in the other ear, lower-SES children did not.[92,93]

Although further research is needed to isolate the components of social status shaping brain structure and functions, convergent evidence from behavioral, fMRI, and ERP studies support the claim that low-SES environments are associated with impairments in attention and executive function.

2.9 Language

Studies exploring the relationship between brain morphometry and SES have also led to the suggestion that low-SES individuals have impairments in brain structures associated with language and reading. Focusing on 10- to 12-year-old children differing in SES (based on parental income), Eckert et al.[94] investigated the relationship between phonological skill (the ability to break down spoken and written words as individual units of sound) and cortical surface area of the left and right planum temporale (regions in the temporal lobe that are highly involved with language processing). Eckert et al.[94] found that, when taking into account SES, planar asymmetry (the difference of left minus right planum temporale surface area, which has been associated with greater phonological awareness[95]) was positively correlated with phonological skill, with low-SES participants showing lower phonological skills and lower asymmetry in the planum temporale. Similarly, evidence from Raizada et al.[90] suggest that possessing higher SES, as determined by a composite of parental income and educational attainment, is associated with a greater degree of hemispheric specialization in Broca's area, or left inferior frontal gyrus, during a rhyming task.

In a study considering the neighborhood SES of participants 35–64 years of age, Krishnadas et al.[96] found that even after controlling for age and alcohol use, participants living in the most deprived neighborhoods have significant cortical thinning in bilateral perisylvian cortices. These brain areas, which divide the frontal and parietal lobes from the temporal lobe below, are believed to be involved in language processing as it relates to verbal short-term memory.[97]

Research by Noble et al.[98] has shown that SES in children, measured as a composite of parental education, occupation, and income-to-needs ratio, can moderate the relationship between certain brain behavior relationships important for reading. Phonological processing ability is positively correlated with activity in the left fusiform and perisylvian cortices, brain areas believed to support learning to read.[99,100] However, Noble et al.[98] have found that this relationship differs among children of high versus low SES. In low-SES children, greater scores in phonological processing strongly predict greater activity in left fusiform and perisylvian regions during reading, whereas in high-SES children, this relationship is less strong. These findings provide further evidence that SES is intertwined with the development of reading and language abilities. Together, these studies indicate that possessing a lower level of SES may result in impaired brain functions related to language and reading, while having a higher level of SES may safeguard individuals from language and reading impairments.

2.10 Stress

A number of studies have suggested that greater exposure to stressors in individuals from low-SES environments can result in changes in neural structures regulating stress response, particularly the hippocampus and amygdala.[74,86,101–103] Impairments in function and development of both the hippocampus and amygdala are important, as they can lead to dysregulation of the hypothalamus-pituitary-adrenal (HPA) axis, one of the systems regulating responses to stressful stimuli.[104]

In a study investigating gray and white matter volume in children 6–12 years old, Luby et al.[39] found that hippocampal and amygdala volumes increased as the income-to-needs ratio of an individual increased. Interestingly, the authors also reported that individuals with greater number of stressful life events could be expected to display greater reduction in hippocampal volume, suggesting that the relationship between the hippocampus and SES may be due to experience- or environment-related stress.

A number of studies have shown reduced hippocampal and amygdala volume in low-SES individuals when assessed based on income, economic hardship, or educational attainment.[40,105–108] These findings are often suggested to be the result of a strong correlation between higher educational attainment and parenting practices promoting socioemotional development, which may have a protective effect on responses to environmental stressors.[47,48,53] Consistent with the idea that educational attainment may be a "proxy" for the quality of home environment, smaller volumes in areas suggested to be related to stress regulation (i.e., hippocampus and amygdala) have been found in individuals from homes with lower educational attainment.[39,40,89,105–109] These data suggest that greater educational attainment may be related not only to greater access to financial resources, but also with a greater ability to deal with stress.[64,109]

Taken together, this research suggests the importance of early factors related to social status on the developmental trajectory of the hippocampus and amygdala. Furthermore, it highlights the possibility that the impaired development of these brain areas in low-SES individuals may result in an impaired ability to respond to later environmental stressors.

2.11 Conclusion

Environmental factors found to associate with social status have important effects on the development, morphology, and function of various brain networks supporting language, attention, executive function, and stress responses. Whereas results may vary based on how researchers characterized SES, these findings indicate that future research integrating neuroimaging methodologies and rigorous examinations of socioeconomic factors should lead to a better understanding of the relationship between social status and brain function. To accomplish this goal, further research may also benefit from investigating the impact of mechanisms related to prenatal and genetic influences. Furthermore, better understanding the impact of social status on social interactions may provide insights into its pervasive role in multiple facets of our lives. Indeed, recent functional neuroimaging investigations suggest that one's own social status and the social status of others shape fundamental social cognitive processes.

3. HOW THE SOCIAL STATUS OF CONSPECIFICS SHAPES PERSON PERCEPTION AND PERSON EVALUATION

As previously mentioned, social status not only impacts cognitive and brain development, but also guides many facets of social behavior.[21,22,35,110–112] A small, but growing, body of neuroimaging research has explored how social status shapes social cognition and provides preliminary insights into how social hierarchies guide how we respond to conspecifics. Once again, because it is such a multifaceted construct, investigations into the neural substrates of social status processing produced a complex pattern of results spanning a number of brain regions. Nonetheless, some of these findings converge to provide insight into how status is identified and impacts evaluations during person perception.

Broadly speaking, areas of the prefrontal, parietal, hippocampal complex, and amygdala appear responsive to variations in the social status of the individuals we perceive. For example, within the prefrontal cortex, the ventral medial prefrontal cortex (VMPFC), ventrolateral prefrontal cortex (VLPFC), dorsolateral prefrontal cortex (DLPFC), and dorsomedial prefrontal cortex (DMPFC) have all been suggested to be recruited when processing the social status of conspecifics.[113–121] Whereas a number of social cognitive processes may be impacted by the availability of social status information, we will focus our review on brain regions believed to support status identification and status-based evaluation (see Figure 1).[114,116]

3.1 Perceived Social Status from Perceptual Cues of Dominance

As previously stated, research to date has construed social status in a number of ways. In some instances, often building upon a rich body of research focused on

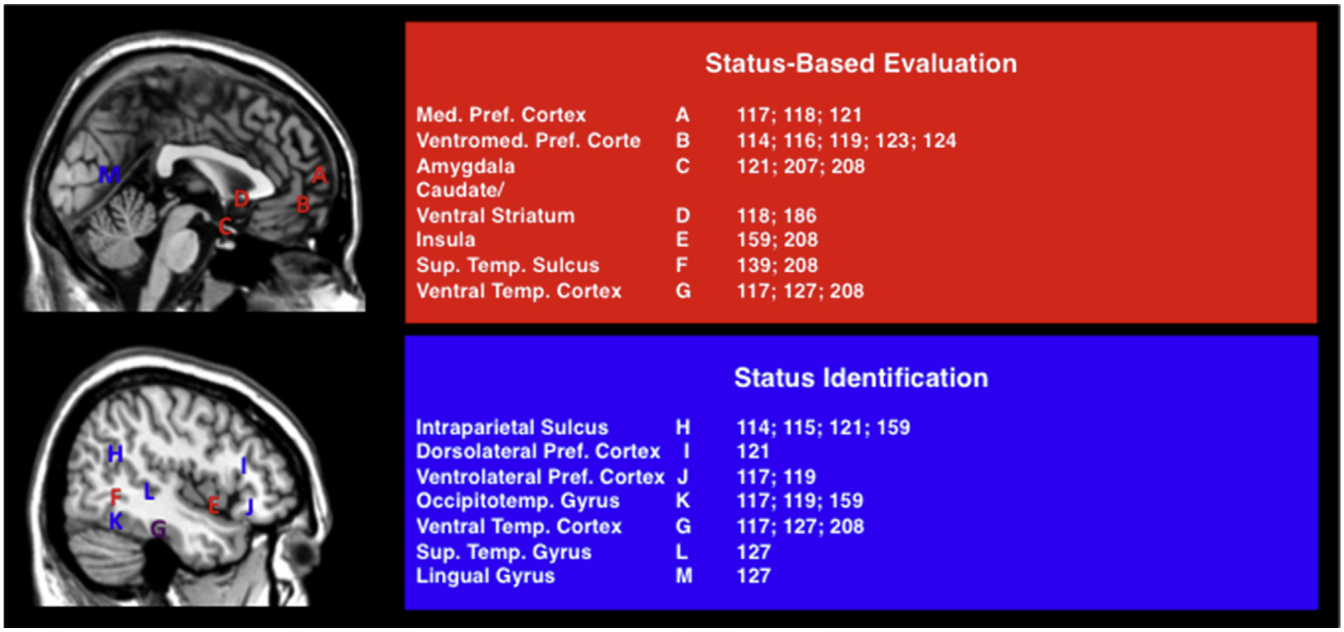

FIGURE 1 Brain regions believed to index status-based evaluation or status identification. Brain regions designated in red have been hypothesized to be involved status-based evaluations. Brain regions designated in blue have been hypothesized to be involved in social status identification.

nonhuman social hierarchies, status is suggested to be identifiable from available perceptual cues (i.e., social dominance).[4,20,119,122–125]

Dominance impacts social organization across a number of species, from ants to nonhuman primates.[2,4,14,20,31,119,122–129] Dominant individuals tend to enjoy greater health, fertility, access to resources, and reproductive success.[14,31,126,128,129] Its impact on human social organization may be less ubiquitous, and the endorsement of dominance as a guiding principle varies considerably across individuals and social groups.[125] Nonetheless, human perceivers readily infer dominance from cues when encountering unknown others.[33,118,119,127,130–136] Dominance can be inferred from static facial cues (i.e., direct eye gaze and upward head tilt), dynamic facial cues (i.e., overt facial anger expressions, speaking quickly and confidently), bodily cues (i.e., crossed arms, open chest, broad shoulders), and perceived nonverbal cues during social interactions (i.e., increased eye contact while speaking compared to listening).[35,118,130–132,137–140] Facial expressions of emotions have also been shown to convey dominance, with expressions of anger being perceived as highly dominant and fearful expressions as highly submissive.[131,132] Given the extent to which social status shapes how we construe others, the efficiency with which we perceive dominance cues in our social environment may not be surprising. Accordingly, recent brain imaging research has begun to explore how the human brain may support social cognitive mechanisms sensitive to variations in the perceived dominance of conspecifics.

In studying the effects of social status on how we perceive others, a number of fMRI studies have focused on the neural underpinnings of perceived dominance from facial expression and body posture.[118,119,127,139] In one such fMRI experiment, Marsh et al.[119] presented photographs of actors varying their gaze orientations, body postures, and gestures to convey low, average, and high dominance to participants who were asked to perform gender judgments. High status was depicted by actors holding their hands behind their back, harboring a dominant facial expression, and generally portraying an "open" body posture. Low status was depicted by actors holding their chin, harboring a submissive facial expression, crossing their legs under their seat, and generally portraying a "closed" body posture. Greater activity in the VLPFC in response to individuals displaying high-status cues, relative to neutral and low-status cues, was observed. The authors suggest that activity in this region may mediate changes in behavior dependent on the social context following status identification. This explanation is consistent with previous work suggesting that the VLPFC is recruited when socioemotional cues, including cues relevant to social hierarchy, are available to influence the selection of appropriate behavioral responses.[117,119,127,141–145] Interestingly, the authors also suggest that the VLPFC/lateral orbitofrontal cortex (OFC) could also be involved in processing the reward value of the targets. Considering that the lateral, in contrast to the medial, OFC has previously been associated with negative evaluations of stimuli,[146,147] it is possible that the dominance portrayed by the high-status individuals may have led to negative evaluations.

Another study examined brain responses to dominance cues in the context of the exploration of cultural differences between individualistic and collectivistic individuals during person perception.[118] Indeed, it has been suggested that American culture tends to place higher value on dominance, whereas Japanese culture tends to reinforce subordinate behavior.[148] In this study, social status was communicated via silhouettes or "figural outlines" that displayed either a dominant body posture (i.e., crossing their arms and looking straight ahead) or a subordinate body posture (i.e., looking down and placing their feet together).[118] The results revealed that American perceivers had greater activation in the caudate and MPFC in response to dominant postures, whereas Japanese perceivers had greater activation in the same brain areas when presented with subordinate postures. The authors interpret these findings to suggest that these brain regions can be flexibly shaped by a cultural tendency to value more dominant or subordinate behavior. Accordingly, the caudate could be involved in learning both the negative and positive value of stimuli during complex social interactions.[149–151] Whereas distinct regions of the MPFC have been found to be involved in mentalizing, self-referential processing, and social evaluations,[152–154] the authors suggest that in the context of their findings, the MPFC may reflect the processing of culturally-specific secondary reinforcers (i.e., dominance for Americans participants and subordination for Japanese participants).[155,156] These findings suggest that response to dominance cues can be flexible and shaped by one's culture and the values it tends to reinforce.

Whereas little research has directly addressed how perceived dominance conveys status in human social hierarchies, the fact that perceptual dominance cues efficiently shape neural responses to others suggest its potential importance in guiding social behavior. Departing from this literature on the perception of dominance, the following sections will review neuroimaging research examining how knowledge of the social standing of others shapes person perception.

3.2 Status Identification and Attention to Social Status

In light of the prevalence of social hierarchies in our lives, it is not surprising that various cognitive and attentional processes have been suggested to be particularly sensitive to the detection of social status. For instance, how we allocate attention toward others is believed to vary as a function of their social status. Although sensitivity to difference in social rank has repeatedly been demonstrated in nonhuman animals,[157,158] it has only recently been systematically investigated in humans. To do so, Foulsham et al.[158] tracked the eye gaze (i.e., frequency and duration of eye movements) of perceivers while they observed individuals of varying social status engaged in a decision-making task (in this study, status was conveyed through peer ratings based on the task performance and leadership abilities of each individual). They found that participants gazed longer and more often at the eyes and faces of high, compared to low, status individuals. Interestingly, recent research suggests that not only are we more likely to orient attention towards high-status conspecifics, but that we also tend to orient our attention in the same direction as them. Indeed, using a gaze-cuing task, Dalmaso et al.[157] found that perceivers shift their attention in response to the averted eye gaze of high-status individuals (in this study status was conveyed through an occupation title presented in a CV).

These findings have been interpreted to suggest that allocating and orienting attention based on social status may be a spontaneous social cognitive skill essential in navigating our social environment. However, only a handful of fMRI studies provide insights into the cognitive processes involved in social status identification. Whereas specific areas of the parietal and prefrontal cortices are typically hypothesized to support status identification, other areas, such as the amygdala, have been shown to be responsive to variations in the social status of others.

Existing research suggests that regions within the parietal cortex are involved in differentiating others based on their social status.[113–115,159,160] More specifically, the intraparietal sulcus (IPS) has been suggested to represent social status. Although this region of the parietal cortex has previously been suggested to support the representation of numerical magnitudes,[161–165] a number of recent studies suggest it may also index social distances, including differences in social status. In one such study, participants were either asked to perform numerical comparisons (by comparing the magnitude of numbers) and social status comparison (by comparing the rank of military positions).[159] The results revealed bilateral IPS activation in response to both numerical and social status comparison. Specifically, greater IPS activity was found when comparing targets closer in distance than those further apart. However, the processes involved in hierarchy differentiation may not be specific to social status comparisons but rather be indicative of the assessments of social distances. Indeed, in another study, participants were asked to either estimate physical distances by indicating which one of two objects is closer to them or social distances by indicating which one of two faces is closer to them.[160] Interestingly, a nearby area of the parietal cortex, the superior parietal lobule (SPL), is also believed to be involved in egocentric representations of spatial information relating external objects to the self.[166,167] Accordingly, it has been proposed that the mental representation of numbers, physical space, and social distance may all share common neural operations supported by the IPS.[159,160,168]

In addition to its involvement in explicit status comparisons, recent studies reveal that areas of the parietal cortex are spontaneously sensitive to social status information when perceiving or interacting with others.[114,121] In one such study, greater IPS activity was found in response to faces paired with low financial status information (e.g., "earns $25,000") compared to those paired with high financial status information (e.g., "earns $350,000").[114] In this study, the participants were never asked to evaluate the social status of the targets and were instead required to form a holistic impression of the individuals.

We replicated and extended these findings in a subsequent study revealing, once again, greater IPS activity in response to faces paired with lower financial status compared to equal and higher financial status, but also greater activity to faces paired with equal and higher moral status compared to lower moral status.[115] Importantly, social status was not conveyed through salary information but instead inferred based on colored backgrounds paired with the faces. For instance, during a prescan training period, darker red backgrounds may have been associated with "lower financial status" (than the participants themselves), whereas lighter red backgrounds may have been associated with "higher financial status." In this case, a darker blue background would have been associated with "lower moral status," while a lighter blue background would have been associated with "higher moral status." These cues were employed to convey levels and types of social status in order to minimize potential confounds associated with the presentation of statements indicating professional occupations or yearly earnings. In contrast to previous research where the status-related information was easily quantifiable, for instance, status based on salary[114] or military rank,[159] this study extends earlier efforts by using status labels that may not as easily lend perceivers to number-processing operations believed to be supported by the IPS.[162–164,169] One possibility is that IPS activity may be indexing the spontaneous assessment of the status of others in comparison to our own.[114,115] The ability to efficiently assess the relative status of conspecifics and their status in relation to our own, and therefore "map-out" a given social hierarchy, may be fundamental to our ability to successfully navigate the social environment. Although this hypothesis seems plausible based on previous research,[114,159,160] future research using larger samples are needed to directly test this potential mechanism.

Assuming the existence of cognitive processes supporting the spontaneous identification of the social status of conspecifics, our response to the social status of others may also depend on the nature of social hierarchical structures.[14,170] Testing this hypothesis, a study by Zink et al.[121] examined how social attention may vary within stable versus unstable social hierarchies. In this study, social status was conveyed by the skill level (e.g., a "one star" for low status versus a "three stars" for high status) of fictitious opponents, depicted via a photograph, with whom the participants were ostensibly playing a game. In reality, the game was simulated and the outcomes were predetermined regardless of participants' actual performance. The results revealed greater activity in the right inferior parietal cortex when participants viewed higher status players relative to lower status ones in a stable hierarchy condition. In contrast, during an unstable hierarchy condition, additional regions, specifically the amygdala and the MPFC (regions suggested to be implicated in social cognition, behavioral readiness, and emotion processing[152,171,172]), were preferentially responsive to viewing high status, compared to low status, players. These findings suggest that perceivers are not only sensitive to others' social rank relative to their own, but that they are also influenced by the stability of the hierarchy. When in an unstable hierarchy, individuals may be more likely to experience emotional arousal stemming, for example, from perceived threats to their relative rank.

3.3 Status-Based Evaluation

Possibly because of the benefits conferred from possessing higher SES in our society, greater social status is often suggested to lead to prestige and positive evaluations from others. Accordingly, individuals with higher status are suggested to be perceived as more competent, valuable to the group, prominent, generous, and reputable, compared to individuals with lower social standing.[35,173–175] However, although social status may influence who we interact with, how we perceive them, and our behavior toward them, we may often be inaccurate when inferring others' personal characteristics based on social status information.[176] Whereas high status may be highly valued by others and confers prestige, it is still unclear whether individuals possessing high social status are consistently evaluated in a positive light. For instance, differences in status-based evaluations may depend on the context in which we encounter others or on the social dimension conferring their status. For example, individuals working on Wall Street may be more likely to be positively evaluated by their peers based on their wealth compared to individuals working for nonprofit charitable organizations.

The characteristics conferring greater status, and possibly positive evaluations, can differ as a function of the nature of social hierarchies. In addition to increased access to material resources, financial status may have such prominence in our society because of the positive life outcomes it confers.[177–181] Nonetheless, whereas high-status individuals may often be evaluated positively, being rich may not necessarily lead to positive evaluations.[182] For instance, rich people tend to be seen as lower in warmth than other social groups.[183]

In contrast, status conferred by relative moral standing, which is suggested to be integral to the maintenance of human social hierarchies,[34,184] may typically lead to positive evaluations and may be detected at an early age.[36,37] In fact, it is conceivable that greater financial wealth may also, in some instances, evoke lower moral status and lead to negative evaluations.[182,183] In contrast, high moral status may confer the respect required to maintain one's standing within hierarchies.[34,175,185]

Recent fMRI investigations suggest that the VMPFC may index status-based evaluations.[114,115,124,186] Lesion studies have involved the VMPFC in processes tied to mentalizing (thinking about the thoughts and feelings of others), emotion processing, decision-making, and person evaluation.[187–190] For example, individuals with damage to the VMPFC show impairments in moral judgment[191] and deficits during facial expressions of emotion recognition tasks.[192,193] Although this region is believed to support numerous social cognitive functions, there is increased evidence suggesting it may index social evaluations in the context of person perception. In the context of social status judgments, evidence derived from human lesion studies suggest that patients with VMPFC damage maintain the ability to recognize social status but exhibit deficits in moral judgment and social norm comprehension.[124] This suggests that the VMPFC may not support cognitive processes related to status identification or differentiation but may instead support the status-based evaluation of others. The VMPFC has been shown to be involved during the evaluation of a wide variety of stimuli.[154,187,194–201] In the context of person perception, fMRI studies suggest that the VMPFC is recruited when individuals are asked to evaluate others.[114,202,203] Interestingly, preferential VMPFC responses are observed not only when evaluating others, but also when reporting one's own affective state.[204,205] The region may integrate affective and social information not only when forming impressions of others, but also when reflecting about the self.

Given its putative involvement in social evaluative processes, it is not surprising that activity in the VMPFC is responsive to the social status of others. In a recent study, greater VMPFC activation was observed in response to individuals paired with high, compared to low, moral status, as indicated by their professional occupation.[114] In this study, participants were shown photographs of faces preceded by information denoting their low or high moral status (e.g., "is a tobacco executive" or "does cancer research"). Once again, participants were asked to form an impression of the targets, not to evaluate their social status. Results revealed that activation of the VMPFC was sensitive to the moral status of individuals, such that higher activation was observed in response to targets paired with person knowledge denoting high moral status, compared to those paired with person knowledge denoting low moral status.

In a subsequent study, we again examined VMPFC response to targets varying in these status dimensions. As previously described, rather than using descriptive knowledge to convey social status, such as pay level or professional occupation, participants were presented with individual faces paired with colored background indicative of a given social status level (high, equal, or low) and dimension (financial or moral) learned during a prescan training session. Analyses revealed an interaction in VMPFC activity between status dimension (financial vs moral) and status level, such that greater activity was not only observed in response to targets with higher compared to lower moral status, as previously shown,[114] but also in response to targets with lower compared to higher financial status. The behavioral evidence collected also revealed that participants judged high moral status individuals to be more likeable. Taken together, these findings suggest that, at least in some contexts, higher status may not always lead to positive evaluations. In fact, supporting previous evidence,[182,183] lower financial status individuals may indeed be evaluated more positively than higher financial status targets.

In addition to the VMPFC, which supports person evaluation and, more generally, the generation of affective meaning,[124,154,202] there are a number of other brain regions that appear to be involved in the perception and evaluation of individuals varying in social status. Although future research will be required to better specify their functions, studies to date suggest that the amygdala, superior temporal sulcus, insula, fusiform gyrus, and lingual gyrus may be components of networks recruited during the processing of information related to social hierarchies.[127,139,206–209]

Whereas brain imaging research covered thus far provides evidence of the impact of social status on brain regions involved in the perception and evaluation of others, a number of studies have also begun to explore how individual differences in the social status of perceivers impact brain responses during social cognitive tasks. The final section in this chapter takes a brief look at this research.

3.4 Individual Differences in Social Status

Recent research has shown different ways in which one's own perceived social status impacts brain activity in response to others.[44,120,186] Muscatell and colleagues[120] explored how subjective social status shapes brain activity when thinking and feeling about others. In the first of two fMRI experiments, participants varying in subjective social status engaged in tasks requiring them to either think about people or objects. The results revealed greater activity in regions previously implicated in the mentalizing network, such as MPFC, posterior Superior Temporal Sulcus (pSTS) and precuneus/posterior Cingulate Cortex (PCC),[210,211] in response to trials in which participants were thinking about people. In addition, a negative correlation was observed between participants' subjective social status and activation in MPFC and precuneus/PCC, such that participants with lower subjective social status exhibited greater activity in these regions. Based on previous work implicating these brain areas in mentalizing processes (thinking about the thoughts and feelings of others)[152] and evidence suggesting that, at least in some contexts, lower status individuals display greater social engagement, empathic accuracy, and perspective taking skills,[212–214] the authors concluded that low-status individuals, relative to their high-status counterparts, may be more likely to focus on others' mental states and infer how they might think and feel.

In their second experiment, Muscatell et al.[120] extended the previous findings by exploring the relationship between perceivers' SES and threat perception. Participants in this experiment were adolescents; therefore, parental income and educational attainment were used to assess their level of SES. When in the scanner, participants were asked to view a series of threatening faces (i.e., facial expressions of anger). In line with previous behavioral findings,[215,216] results revealed a negative correlation between participants' social status and brain activation in regions of interest, such that perceivers with lower SES tended to have increased activity in the MPFC and left amygdala in response to threatening images relative to a fixation baseline. The authors interpret these results as evidence of a relationship between social status and the recruitment of brain regions involved both in mentalizing (i.e., MPFC) and threat detection (i.e., amygdala). Similar to the first study, they suggest that those lower in social status may have greater abilities to recognize others' mental and emotional states.

Finally, a recent study explored how the subjective social status of perceivers may impact reward responses when processing information about others varying in social status. In this study, Ly et al.[186] found that viewing individuals of the same rank as oneself elicited greater activity in the ventral striatum, an area widely associated with reward processing. During an fMRI session, participants were shown two faces serially along with a caption indicating whether the individual had a higher or lower social status than them. Following the serial presentation of these faces, the two faces were presented one above the other along with a statement (i.e., which person has been fired from more than one job?). Participants were then instructed to indicate to which of the two individuals the statement was more likely to pertain. The results revealed that participants' subjective social status was associated with differences in ventral striatal activity in response to information paired with either high or low-status targets. More specifically, perceivers who reported higher subjective social status demonstrated greater ventral striatal responses to targets of higher status, whereas participants with low subjective social status displayed greater ventral striatal activity when viewing targets of lower status. In contrast to work with nonhuman primates suggesting that higher status conspecifics may typically elicit greater reward responses,[16–20] these findings suggest that individuals with similar social statuses may be more rewarding. Taken together, the results of these three experiments suggest that our own social status shapes how we respond to others.

4. TOWARDS AN INTEGRATION OF BRAIN IMAGING INVESTIGATIONS OF SOCIAL STATUS

Initial brain imaging efforts suggest that social hierarchies and social status impact cognitive functioning, shape brain structures, and impact the neural substrates of person perception and evaluation. Although the previously described findings are indicative of progress toward our understanding of how this important construct shapes us and our response to others, much remains to be done to better understand the neural processes at play and to integrate these findings across many relevant research areas.

For example, according to a status characteristics theory,[217] higher social status is associated with certain social groups, such as being white, male, middle-aged, having higher educational attainment, and having greater occupational prestige. Although, as discussed, income, education, and occupation are commonly used as objective markers of social status, race and gender may also serve as status cues (in a similar way dominance cues are suggested to indicate social status) and interact with other status indicators during person perception and evaluation.[123] Indeed, in the context of contemporary American culture, social status and race are often intertwined. Members of racial minority groups, such as African Americans, are often assumed to be socially disadvantaged, whereas white individuals are often assumed to possess high status.[218] Future studies may benefit from exploring the interaction of race and gender with various indicators of social status to better understand the variables shaping the distributed network of brain regions involved in person perception. When doing so, important individual differences, such as contact to racial outgroup members[219] and endorsement of status-legitimizing beliefs, should be considered.[220] For example, research suggests that whites endorsing status-legitimizing beliefs view rises in social status of black individuals as threatening.[218] Similarly, males who endorse social dominance orientation to a greater extent demonstrate greater gender differences in issues relevant to gender equity.[221] Accordingly, group membership (i.e., gender and race) may often impact how social status guides person perception and, therefore, research considering both the social status of targets and their gender and race is needed.

In recent years, a large body of literature has uncovered the detrimental effects of subjective social status on health, even after controlling for objective measures, such as socioeconomic status.[14,170,222,223] A meta-analysis conducted by Thayer et al.[224] identified that changes in the autonomic nervous system, suggested by some to index potential detrimental effects of possessing lower SES, are associated with brain regions involved in emotional processing, such as the amygdala and the MPFC. Indeed, greater exposure to stressors associated with possessing a lower social status can cause structural and functional changes in the brain and predisposes the brain to a disrupted stress response.[102,225–227] Stress-related responses in the neuroendocrine system, the autonomic nervous system, and the immune system occur in order to protect an organism against these adversities in life, a process often called "allostasis."[102,228] Although these physiological adaptations are beneficial in the short run, allostatic load in the face of chronic stress may lead to worse health over an extended period of time.

In addition to investigating how environmental factors associated with possessing lower SES impact stress-related health outcomes, social cognitive investigations integrating behavioral, psychophysiological, and brain imaging methodologies may be beneficial to our understanding of the dynamic mechanism by which social status impacts function.[229] Indeed, one possibility is that VMPFC activity indexing status-based evaluations may also provide important indications of psychophysiological responses to others varying in social status.[116,230,231]

Brain imaging investigation of social hierarchies and social status has made great strides in recent years, but it remains highly underrepresented in the literature. We suspect that the great variability in definitions used when investigating both the impact of SES on brain functions and the impact of status on social cognition greatly contributes to this state of affairs. Nonetheless, with its immense relevance to central aspects of stress, coping, and health, as well as to social cognition, it seems essential to tackle these difficulties and move forward in our understanding of the pervasive impact that social status has on human life.

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