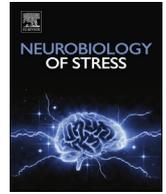




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Social inequalities in health in nonhuman primates

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ABSTRACT

Overall health has been linked to socioeconomic status, with the gap between social strata increasing each year. Studying the impact of social position on health and biological functioning in nonhuman primates has allowed researchers to model the human condition while avoiding ethical complexities or other difficulties characteristic of human studies. Using female cynomolgus macaques (*Macaca fascicularis*), our lab has examined the link between social status and stress for 30 years. Female nonhuman primates are especially sensitive to social stressors which can deleteriously affect reproductive health, leading to harmful consequences to their overall health. Subordinates have lower progesterone concentrations during the luteal phase of menstrual cycle, which is indicative of absence or impairment of ovulation. Subordinate animals receive more aggression, less affiliative attention, and are more likely to exhibit depressive behaviors. They also express higher stress-related biomarkers such as increased heart rates and lower mean cortisol. While no differences in body weight between dominant and subordinate animals are observed, subordinates have lower bone density and more visceral fat than their dominant counterparts. The latter increases risk for developing inflammatory diseases. Differences are also observed in neurological and autonomic function. A growing body of data suggests that diet composition may amplify or diminish physiological stress responses which have deleterious effects on health. More experimental investigation of the health effects of diet pattern is needed to further elucidate these differences in an ongoing search to find realistic and long-term solutions to the declining health of individuals living across the ever widening socioeconomic spectrum.

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1. Introduction

1.1. Socioeconomic status and health

A strong gradient in health parallels the socioeconomic gradient in human society. Health disparities across social strata grow larger each year, and there have been a great deal of clinical and epidemiological research directed toward understanding the causes of this growing inequality. Important contributors that have been identified include social determinants such as health-related features of neighborhoods (e.g. walkability, recreational areas, accessibility to healthy food), socioeconomic factors (e.g. income, wealth,

and education) (Braveman and Gottlieb, Jan–Feb 2014), discrimination, and social capital (Braveman et al., 2011) (Uphoff et al., 2013). The proximal effect these factors have in common is that when experienced chronically they may promote or buffer physiological responses which damage health (Braveman et al., 2011) (Chen and Miller, 2013). Socioeconomic status is inversely associated with level of chronic social stress (AdlerRehkopf, 2008). Several decades of research, spanning basic science to epidemiological levels of analysis, have repeatedly identified a sense of control over the environment and social supports as important moderators of the physiological impact of stressful life events (Matthews and Gallo, 2011).

1.2. Characteristics of primate social status hierarchies

The social status hierarchy is a central organizing feature in the societies of most species living in groups larger than the nuclear family. Some characteristics of social status are shared across species. For example, high social status confers priority of access to resources such as food, water, safe resting sites, and mates (Fig. 1A).

Abbreviations: HR, Heart rate; HPA, Hypothalamic-pituitary-adrenal; ACTH, Adrenocorticotropic hormone; TPH, Tryptophan hydroxylase; 5-HT, Serotonin; HVA, Homovanillic acid; CSF, Cerebrospinal fluid; PET, Positron emission tomography; CAA, Coronary artery atherosclerosis; CRH, Corticotropin-releasing hormone; IGF-1, Insulin-like growth factor-1; TPC, Total plasma cholesterol; HDL-C, High-density lipoprotein cholesterol; ANS, Autonomic nervous system.

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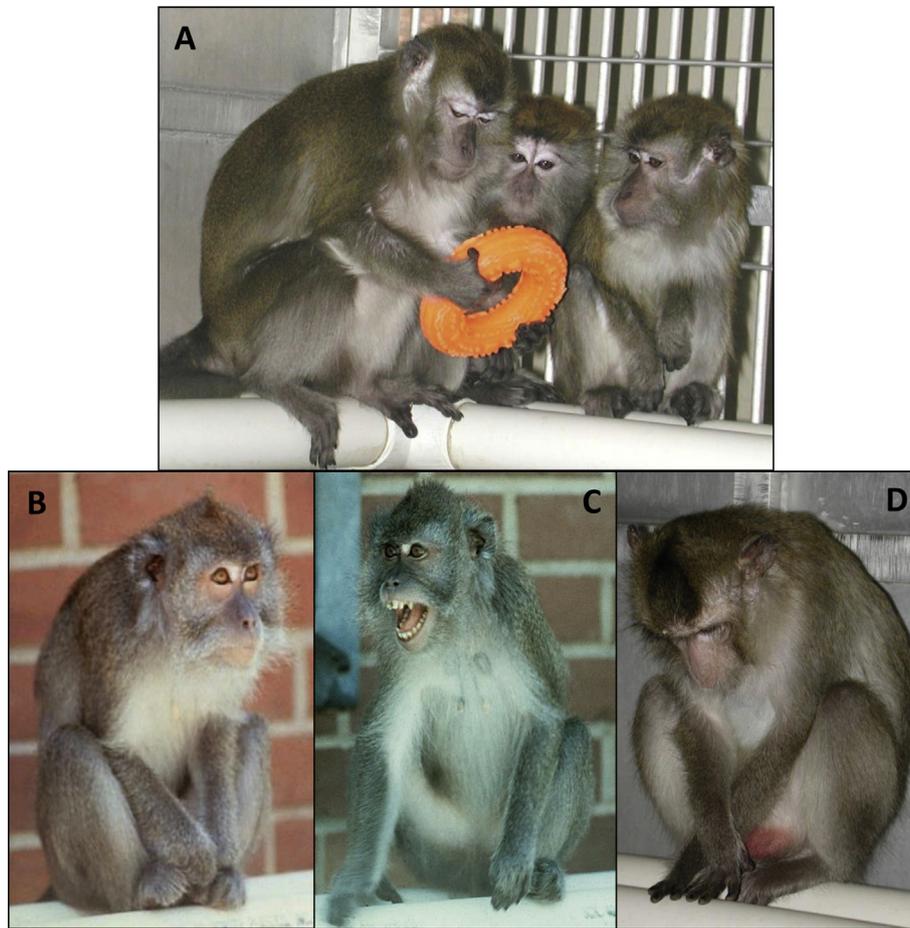


Fig. 1. Behaviors Associated with Social Status. **A:** High social status confers priority of access to resources; **B:** Vigilant scanning of the social environment is characteristic of subordinates; **C:** Subordinates receive more aggression from more dominant monkeys; **D:** Subordinates are more likely than dominants to exhibit depressive behavior which includes a slumped or collapsed body posture (head below shoulders), with open eyes, accompanied by a lack of responsiveness to environmental events (Shively et al., Apr 15 1997).

When resources are abundant there is little difference between high and low status individuals in access to resources. However, when resources become scarce, such as during drought or famine, social status may determine whether an individual can obtain enough food or water to maintain the degree of good health necessary to reproduce, or survive (Sapolsky, Apr 29 2005). High social status also confers a relatively more predictable social environment – dominants can have what they want, when they want it. Subordinates depend upon the largess of dominant animals for access to necessary resources which may be withdrawn at any time. Subordinates also may be subject to aggression at any given moment (Fig. 1B, C). In general the offspring of subordinates are also subordinate, at least while dependent on their parent(s), and share low priority of access to resources and a relatively unpredictable social environment (Shively, 1985). This situation creates the opportunity for both genetic and nongenetic transmission of traits along social status lines. These basic characteristics of social status set the stage for social inequalities in health.

1.3. Social suppression of reproductive function

It is imperative for female mammals to be sensitive to the current physical and social environment because of the enormous investment they make in each offspring. When resources are scarce it is a better strategy to divert energy from reproduction to physiologic processes designed to keep the individual alive; when resources are plentiful reproduction is favored. Compared to

dominants, subordinate female mammals may experience more reproductive system dysfunction, which in turn may impact other aspects of health. Thus, females appear to be sensitive to environmental characteristics which may influence reproductive outcomes (Beehner and Lu, Sep–Oct 2013).

1.4. Translational studies of social status effects on health

Social status hierarchies in human societies share most of these basic characteristics. Studying the impact of social position on health and biological functioning in other gregarious species may give us insight on the human condition without the ethical complexities of studying human behavior *in situ*. Studying the impact of social status on health in a laboratory environment affords tighter controls over confounding factors such as status differences in physical environments, food quality and accessibility, ethnicity, and health care allowing for a focused evaluation of the biological impact of social status differentials.

2. Social status and stress in cynomolgus macaque social groups

2.1. Social status in cynomolgus macaque society

In the wild, cynomolgus monkeys (*Macaca fascicularis*) live in groups comprised of one or more adult males, multiple adult females, and their dependent offspring. Males are usually not related

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