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Relationships between affiliative social behavior and hair cortisol concentrations in semi-free ranging rhesus monkeys

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ABSTRACT

Sociality is a fundamental aspect of human behavior and health. One benefit of affiliative social relationships is reduced short-term levels of glucocorticoids (GCs), which are indicative of physiological stress. Less is known, however, about chronic GC production in relation to affiliative social behavior. To address this issue, we studied a semi-free ranging troop of rhesus macaques (*Macaca mulatta*) and collected hair samples to measure hair cortisol concentrations (HCCs), as a measure of chronic GC production, during routine biannual exams. We collected social behavior (both aggressive and affiliative) and hair samples for 32 adult female rhesus macaques over one year (Experiment 1). Our results indicated that adult females who initiated higher levels of social affiliation had significantly lower levels of HCCs. Neither the initiation nor the receipt of aggression were significantly related to HCCs in this study. In a second experiment we studied 28 mother-infant dyads for the first 90 days postpartum to examine mother-infant facial interactions (i.e. mutual gazing). We analyzed HCCs during weaning approximately one year later, which is a major transitional period. We found that infants that engaged in higher levels of mutual gazing in the first 90 days postpartum had significantly lower levels of HCCs during weaning. Finally, we studied 17 infant rhesus macaques (13 males) to examine whether social behavior (such as play) in the first five months of life correlated with infant HCCs over those months (Experiment 3). We found that infant males that engaged in more social play had significantly lower levels of HCCs. By relying on an animal model, our study shows that affiliative social traits are associated with lower long-term GC production. Future research should address the complex interactions between social behavior, chronic GC production, and mental and physical health.

1. Introduction

Group living mammals have developed a complex system of social interactions that have evolved to create stable social bonds over time, which have reproductive and lifespan-extension benefits (Kappeler et al., 2015; Silk et al., 2010). For example, individuals with strong social bonds live longer (Silk et al., 2010; Yee et al., 2008), possibly because social support has been linked to lower disease risks (Seeman, 1996) and faster recovery (Kulik and Mahler, 1989). The health benefits of affiliative social relationships are also likely related to reduced levels of circulating glucocorticoids (GCs), hormones that participate in the physiological stress response, that result from affiliative social interactions (Heinrichs et al., 2003; Shutt et al., 2007). Indeed, chronic high levels of circulating GCs can result in cardiovascular impairments, reproductive inhibition, immunosuppression (Sapolsky, 2005), and neurobiological changes such as dendritic atrophy, which is a risk factor for depression (Qiao et al., 2016). Moreover, loneliness, or perceived social isolation, is a risk factor for mental and physical health issues (Hawkley and Cacioppo, 2013).

Studies examining sociality and endocrine measures of stress have relied on short-term samples of GCs, which are typically collected from urine, feces, saliva, and blood and are subject to a number of confounds including circadian rhythm, temporal restrictions, and environmental variability (Davenport et al., 2006; Meyer and Novak, 2012). Additionally, these samples relay little information about chronic hypothalamic-pituitary-adrenocortical (HPA) axis activity, unless

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numerous sequential samples are taken over time, which can pose various challenges (Davenport et al., 2006).

A recent tool to measure chronic HPA axis activity is the collection of hair to quantify hair cortisol concentrations (HCCs; Davenport et al., 2006; Meyer and Novak, 2012). Hair reflects chronic retrospective HPA axis activity over a period of weeks to months without the need for multiple samplings. HCCs have been increasingly relied upon in both animal and human biobehavioral research, and studies have revealed relationships between HCCs and mental disorders such as depression (Qin et al., 2015) and generalized anxiety disorder (Staufenbiel et al., 2013), as well as physical disorders such as cardiovascular disease (Manenschijn et al., 2013) and myocardial infarction (Pereg et al., 2011). In addition, HCCs may be a biomarker of major life stressors (Karlén et al., 2011) such as childhood abuse (Schreier et al., 2015) and chronic stress in dementia caregivers (Stalder et al., 2014). However, inconsistent results between self-reported stress and HCCs have been found in humans (associations: Gow et al., 2011; Kalra et al., 2007; Qi et al., 2014; no associations: O'Brien et al., 2013; Olstad et al., 2016; Stalder et al., 2010, 2017; Wells et al., 2014), with researchers hypothesizing that subjective measures do not capture experiences of stress in the same way as physiological measures (Olstad et al., 2016). Indeed, studies utilizing more objective measures have established relationships with HCCs (Geng et al., 2016; Stalder et al., 2017). One objective measure may be overt social behavior, such as measured frequencies of aggression and affiliation. In this regard, several recent studies have begun examining the relationships between aggression and HCCs in mammals (Feng et al., 2016; Salas et al., 2016; Tennenhouse et al., 2016; Yamanashi et al., 2016). However, even though affiliation plays a fundamental role in social organization in humans and nonhuman primates, little research has examined the relationship between affiliation and chronic HPA axis activation.

One particular type of affiliative social behavior that has not been examined with respect to HCCs is the influence of maternal interactions. Previous research in animal models has suggested that mothers act as a buffering mechanism for stressors in infants, and infants who are deprived maternal care may lack the ability to regulate the HPA system (Dettmer et al., 2012, 2016a; Feng et al., 2011; Hennessy et al., 2009). However, less is known about how natural variations in maternal care, rather than the lack of maternal care *per se*, as well as other social behaviors such as play, relate to long-term HPA axis activity. Addressing this gap will elucidate the impacts that variable maternal care has on downstream infant HPA axis regulation and social development.

To address these literature gaps, we studied social behavior and HCCs in a troop of rhesus macaques (*Macaca mulatta*) living in a naturalistic, semi-free ranging environment. Rhesus macaques are an ideal animal model for these processes in humans because they have natural variations in the tendency of affiliation (Capitanio et al., 2014) and maternal behavior (McCormack et al., 2006), and they form strict dominance hierarchies characterized by frequent aggression. Aggression may be seen as a proxy for bullying in humans, which has also been related to GCs (Hansen et al., 2006.) In Experiment 1, we studied 32 adult female rhesus macaques over one year. We predicted that 1) high rates of received aggression would be associated with higher levels of HCCs, and 2) high rates of affiliation would conversely be associated with lower levels of HCCs. In Experiment 2, we studied 28 mother-infant dyads for the first 90 days postpartum to determine the relationship between early mother-infant face-to-face interactions (i.e. mutual gazing: Dettmer et al., 2016b, 2016c; Ferrari et al., 2009) and later offspring HCCs. Hair samples were obtained at routine semiannual health exams. We analyzed the hair samples taken at weaning age, which typically occurs after the birth of their next sibling, at an average of 12 months of age (Fooden, 2000). Because the transition from nursing to a weanling is a period of marked maternal-infant conflict (Trivers, 1974), we sought to explore whether variations in early maternal face-to-face interactions would relate to infant HPA axis regulation during this critical time of development. We therefore predicted that 3) higher frequencies of mutual gazing after birth would negatively correspond with HCCs during the time of weaning. In Experiment 3, we studied 17 infant rhesus macaques throughout the first five months of life to report on the relationship between infant social behavior and HCCs. We predicted that 4) infant social behavior, particularly social play (the most frequent peer-to-peer behavior at this age), would negatively relate to HCCs.

2. Methods

2.1. Subjects and housing

In Experiment 1, subjects were 32 adult female rhesus macaques (age range: 3–18 years; mean ± SD: 8.19 ± 3.34 years) observed from August 2014 to August 2015. The females represented all major lineages (i.e., matrilines; N = 3) in the troop (matriline 3: N = 19; matriline 4: N = 11, matriline 1: N = 2). In Experiment 2, subjects were 28 mother-infant dyads (16 female infants; 12 males) studied in the first 90 days postpartum in 2013 and 2014. In Experiment 3, subjects were 17 infant rhesus macaques (13 males, 4 females) born between March and May 2015 and studied from birth through August 2015. All subjects were born and reared at the Laboratory of Comparative Ethology (LCE) field station at the NIH Animal Center in Poolesville, Maryland. The field station was a 5-acre (2.0 ha) open-air enclosure with natural vegetation, a pond (0.9 ha) with a centralized island (0.07 ha), and climbing structures and enrichment. Three corncrib shelters (4.88 × 4.88 × 5.79 m) and three indoor climate controlled runs (2.74 × 5.79 × 4.27 m) provided protection from inclement weather. Commercial lab diet (Purina Monkey Chow #5038, St. Louis, MO), natural vegetation, and water were available *ad libitum* and supplemented with fresh fruits and seeds/nuts twice a day. All procedures described below adhered to the NIH Guide for the Care and Use of Laboratory Animals and were approved by the NICHD Animal Care and Use Committee (ACUC).

2.2. Data collection

2.2.1. Experiment 1: aggression

A total of 4898 dominance interactions were recorded from August 2014 to August 2015 through both focal and *ad libitum* sampling (Altmann, 1974). Interactions included both aggressive (threat, chase, attack) and submissive interactions (fear grimace, displacement; see Wooddell et al., 2016). Dominance ranks were established via Elo-rating (Neumann et al., 2011; Wooddell et al., 2016).

2.2.2. Experiment 1 and 3: adult and infant focal behavioral data

Adult behavioral data were collected via modified frequency sheets (Novak et al., 1998; Wooddell et al., 2016) by two primary observers (LJW and AMD; inter-rater reliability ≥ 85%) from August 11, 2014 through August 10, 2015 using a 5-min continuous focal animal sampling method (Altmann, 1974). Each 5-min session was divided into 20, 15-s intervals. Any behavior that occurred within the 15-s was recorded in chronological order. The maximum frequency a behavior could occur therefore was 20 intervals per session. Each female (N = 32) was coded for 1–2 sessions per week in both morning (900–1200) and afternoon sessions (1200–1700). A total of 1833 adult observations (mean ± SEM: 57.28 ± 3.55 sessions per female) were collected during the study period, totaling 153 h. Each infant born in 2015 received three weekly sessions following this coding scheme starting at approximately one month of age. A total of 446 infant focal observations (mean ± SEM: 26.23 ± 0.24 sessions per infant) were collected during the study period, totaling approximately 37 h. Total focal data collection time (for both adults and infants) thus was approximately 190 h.

Behaviors collected included nonsocial behaviors (locomotion, foraging, etc.) and social behaviors. For the purposes of this study, we