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Reunion behavior after social separation is associated with enhanced HPA recovery in young marmoset monkeys

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Summary The relationships that offspring develop with caregivers can exert a powerful influence on behavior and physiology, including the hypothalamic-pituitary-adrenal (HPA) axis. In many mammalian species, offspring—caregiver relationships are largely limited to interactions with mother. Marmoset monkeys receive care in early life from multiple classes of caregivers in addition to the mother, including fathers and siblings. We evaluated whether affiliative social interactions with family members in marmosets were associated with differences in cortisol reactivity to a short-term social separation stressor, and whether these variations in affiliative interactions upon reunion predicted how well marmosets subsequently regulated HPA axis function after cessation of the stressor. Marmosets were separated from the family for 8 h at three developmental time points (6-, 12-, and 18-months of age), and interactions of the separated marmoset with the family group were recorded during reunion. Urinary cortisol was measured prior to social separation, every 2 h during the separation, and on the morning after separation. Heightened cortisol reactivity during social separation did not predict affiliative social behavior upon reunion but higher rates of grooming and play behavior predicted enhanced HPA regulation. Marmosets with higher rates of grooming and play with family members upon reunion had post-stress cortisol levels closer to preseparation baseline than marmosets with lower rates of affiliative reunion behavior. Combined with previous research showing the early programming effects of social interactions with caregivers, as well as the buffering effect of a close social partner during stress, the current study highlights the high degree of behavioral and HPA adaptability to social stressors across development in marmoset monkeys.

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1. Introduction

In primates, infants spend early developmental periods in close contact with caregivers and often maintain close social relationships with caregivers throughout development and into adulthood. Not surprisingly, social separation in young monkeys reliably produces increases in hypothalamic-pituitary-adrenal (HPA) activity (and its primary output, cortisol) and anxiety-like behavior, and has been a standard laboratory method of inducing stress responses in primates (Coe et al., 1983; Dettling et al., 2002; French et al., 2012; Gunnar et al., 1981). Despite these rapid separation-induced changes in behavior and HPA function, reunion with caregivers quickly alleviates the effects of separation. Reunion with caregivers results in cessation of stressor-induced behavior, and a return to baseline HPA function and social behavior (Dettling et al., 1998, 2002; French et al., 2012). The speed of this return to baseline is dependent on the severity of the stressor. For example, capture and brief handling usually produces an increase in cortisol in young squirrel monkeys, but if a juvenile is captured, handled, and then immediately returned to the mother, this cortisol response is blunted (Levine et al., 1978; Mendoza et al., 1978; Wiener et al., 1987). If the separation is prolonged though, cortisol can remain elevated for 30 min to 12 h after reunion with the caregiver (French et al., 2012; Levine et al., 1978), returning to normal levels within 2 days (Cinini et al., 2014). Additionally, reunion with a caregiver causes reductions in stressor-induced behavior, and increases in novelty exploration and peer-directed social behavior (Dettling et al., 1998, 2002; Erickson et al., 2005). Clearly there are properties of the reunion experience that serve to terminate stress activation and begin behavioral and physiological regulation.

Parents and peers can serve as powerful social buffers during stressful situations, and they can also serve as regulators of physiological function following a stressor (DeVries et al., 2003; Hostinar et al., 2014). Maintaining some contact with a caregiver can help to buffer the effects of social separation. For example, moving young monkeys from group housing to single housing causes increases in cortisol, but if the mother is relocated with the infant, this response is blunted (Wiener et al., 1987). Similarly, compared to total social separation, the cortisol response is blunted when young monkeys are removed from the home cage and housed adjacent to the mother (Bayart et al., 1990; Levine et al., 1985). Even limited communication (olfactory and auditory) between a mother-infant pair partly attenuates the cortisol response to separation in young squirrel monkeys (Levine et al., 1993). Behaviorally, infants engage in more time in contact with the mother following exposure to novelty stress if exposed to novelty alone, relative to when exposed to novelty with the mother present (Parker et al., 2006). There are also effects of early social environment on social buffering. When mother-reared macaques are separated from the group with a partner, they engage in more social contact behavior, and have lower cortisol than nursery reared macaques (Winslow et al., 2003). Similarly, infant squirrel monkeys exposed to an early stress-inoculation paradigm, in which young monkeys are repeatedly exposed to a mild separation stressor followed by maternal reunion, are less neophobic than normally reared monkeys when exposed to novelty with the mother present (Parker et al., 2006).

In addition to these social effects on HPA activity and behavior *during* exposure to stressors, social interactions with a caregiver that *follow* a stressor can also modulate HPA activity. In squirrel monkeys, longer nursing duration immediately following separation is associated with lower plasma cortisol and ACTH (Parker et al., 2006). Behaviorally, young monkeys seek out contact with the caregiver upon reunion, and monkeys that exhibit greater behavioral agitation during the stressor have longer durations in contact with the mother (Dettling et al., 1998; Gunnar et al., 1981). Thus it is clear that contact with the caregiver during and after a stressor can alter behavioral and HPA responses to stressors in young primates.

Infants develop a strong social bond with the primary caregiver, and in most nonhuman primates, the primary caregiver is the mother. In contrast to macaques and squirrel monkeys, marmosets develop within a family unit in which they can interact with caregivers of varied ages and sexes (French, 1997; Nunes et al., 2001; Tardif, 1997). Additionally, the HPA system in developing marmosets is highly sensitive to familial social influences (Birnie et al., 2013; Dettling et al., 2002; Mustoe et al., 2014). The purpose of the current study was to examine relationships among affiliative sociality, HPA activity and behavior along a shorter timescale. We separated young marmosets from their family groups and evaluated whether HPA reactivity during the stressor was related to affiliative reunion behavior. We also assessed whether marmosets who engaged in more affiliative behavior during reunion subsequently returned to baseline HPA functioning in the hours following the stressor. Specifically, we predicted that if engagement in affiliative social interactions with the family is a normative response to stressors, then marmosets that exhibit higher cortisol responses to separation stress would engage in higher rates of grooming and play with family members upon reunion. We also predicted that if social interactions with the family serve an important regulatory role in HPA function following the cessation of a stressor, then marmosets that participated in more grooming and play during reunion would display cortisol values closer to baseline levels after 24 h post-separation.

2. Method

2.1. Subjects

A total of 52 marmosets (*Callithrix geoffroyi*; 30 males, 22 females) were tested at three developmental time points (6, 12, and 18 months of age). These time points were chosen as distinct developmental stages: *juvenile*, *sub-adult*, and *young adult* (Yamamoto, 1993). Subject attrition from the study lead to different samples sizes at each age in which complete behavioral and endocrine data were available: 6 months ($n = 44$), 12 months ($n = 40$), and 18 months ($n = 29$). Marmosets that were removed from the study did not differ from those that remained on any behavioral or endocrine measures ($ts < \pm 1.62$, $ps > .11$) Marmosets were housed in family groups composed of a breeding pair and their offspring (mean number of