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Review article

Neuroendocrine control in social relationships in non-human primates: Field based evidence

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ABSTRACT

Primates maintain a variety of social relationships and these can have fitness consequences. Research has established that different types of social relationships are unpinned by different or interacting hormonal systems, for example, the neuropeptide oxytocin influences social bonding, the steroid hormone testosterone influences dominance relationships, and paternal care is characterized by high oxytocin and low testosterone. Although the oxytocinergic system influences social bonding, it can support different types of social bonds in different species, whether pair bonds, parent-offspring bonds or friendships. It seems that selection processes shape social and mating systems and their interactions with neuroendocrine pathways. Within species, there are individual differences in the development of the neuroendocrine system: the social environment individuals are exposed to during ontogeny alters their neuroendocrine and socio-cognitive development, and later, their social interactions as adults. Within individuals, neuroendocrine systems can also have short-term effects, impacting on social interactions, such as those during hunting, intergroup encounters or food sharing, or the likelihood of cooperating, winning or losing. To understand these highly dynamic processes, extending research beyond animals in laboratory settings to wild animals living within their natural social and ecological setting may bring insights that are otherwise unreachable. Field endocrinology with neuropeptides is still emerging. We review the current status of this research, informed by laboratory studies, and identify questions particularly suited to future field studies. We focus on primate social relationships, specifically social bonds (mother-offspring, father-offspring, cooperative breeders, pair bonds and adult platonic friendships), dominance, cooperation and in-group/out-group relationships, and examine evidence with respect to the 'tend and defend' hypothesis.

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1. Introduction

Social relationships are formed through repeated social interactions between the same individuals (Hinde, 1983, Cheney and Seyfarth, 1986). In mammals, social relationships are underpinned by a number of neuroendocrinological systems (Broad et al., 2006a, 2006b; Maestripieri, 2010; van Anders et al., 2011; Goodson, 2013; Chang et al., 2013; Brent et al., 2014; Rilling and Young, 2014; Crespi, 2015; Numan and Young, 2016). Over the last couple of decades, laboratory research has led to increased understanding of the functions, effects, and interactions of different hormones in the body and brain, and their impact on emotions, social cognition, behavior and social interactions. How this complex interplay of hormones, brain activity and behavior contributes to the formation and maintenance of different types of social relationships is beginning to be understood (Broad et al., 2006a, 2006b; Maestripieri, 2010; van Anders et al., 2011; Goodson, 2013; Chang et al., 2013; Brent et al., 2014; Rilling and Young, 2014; Crespi, 2015; Numan and Young, 2016).

One prevalent type of social relationship is the social bond, in which an animal shows a preference or selectivity to affiliate with a particular individual. Social bonds can occur between kin: mothers or fathers and their offspring, family groups, or within cooperative breeding groups (Silk et al., 2009; Cheney and Seyfarth, 2008; Snowdon, 2015), between breeding pairs, and in platonic friendships between unrelated adults (Snowdon, 2015; Langergraber et al., 2007, 2009; Schülke et al., 2010). Another prevalent type of social relationship is based on shows of dominance and subordination resulting in dominance relationships (Bergman et al., 2003; Cheney and Seyfarth, 2008). Relationships between social groups also exist, and are defined by hostility in the case of territorial species, or neutral or affiliative interactions in less territorial species (Wrangham, 1980; Herbinger et al., 2001).

Broadly speaking, clarity is emerging in terms of which endocrine systems are principally involved in which types of relationships. Social bonds are influenced by neuropeptides, such as oxytocin, vasopressin and prolactin (Rilling and Young, 2014; Storey and Ziegler, 2016). Oxytocin, for example, fosters partner-specific preferences for affiliation, and is key in facilitating mother-offspring bonds (Rilling and Young, 2014). Testosterone mediates dominance relationships (Muller, 2017, this issue). However, less is known about how hormones interact, such as between oxytocin and testosterone, or each of these hormones with the HPA axis (van Anders et al., 2011; Carter, 2014; Crespi, 2015; Trumble et al., 2015).

Not only social relationships but also certain contexts or behaviors can trigger the release of hormones, precipitating positive or negative feedback loops or cascade reactions that can down or up regulate other hormones. For example, in some contexts, oxytocin release may be subject to a positive feedback mechanism whereby oxytocin may promote affiliative behavior, which may in turn promote further oxytocin release. Oxytocin simultaneously down-regulates HPA axis activity (Bethlehem et al., 2014; Sanchez et al., 2015), such as occurs during social buffering. Here, during exposure to a stressor, affiliation or support from a bond partner that triggers oxytocin release, may result in reduced cortisol release (Heinrichs et al., 2003; Sanchez et al., 2015 Cavanaugh et al., 2016; Wittig et al., 2016). However, hormonal interactions are not yet fully understood. In some contexts, hormones seem to oppose each other, such as the low testosterone and high oxytocin levels observed during early fatherhood. In other contexts, the same hormones seem to facilitate each other (Trumble et al., 2015). Sexual activity, hunting and in-group/out-group contexts, for example, involve simultaneously high oxytocin, testosterone and glucocorticoid concentrations (Sobolewski et al., 2012a; Sobolewski, 2012b; Trumble et al., 2015; Wittig et al., 2016; Samuni et al., 2017).The resulting social behavior from hormonal interactions priming or suppressing activation in specific brain areas (Donaldson and Young, 2008; Rilling and Young, 2014; Bosch et al., 2016), can facilitate or impede cooperation (Soares et al., 2010; Trumble et al., 2015), contest (Beehner et al., 2006), or responses to stressors (Hennessy et al., 2009; Young et al., 2014; Wittig et al., 2016), which likely facilitate or impede relationships such as social bonds (Cacioppo et al., 2015).

While the processes between neuroendocrine systems and behavior are highly conserved across mammals, from rodents to humans, functional shifts are apparent between species (Goodson, 2013). For example, in two closely related rodent species, prairie voles (*Microtus ochrogaster*) and meadow voles (*Microtus pennsylvanicus*), maternal care of offspring is facilitated by oxytocin circuitry. However, only prairie voles form pair bonds, and only in this species, does oxytocin circuitry facilitate partner-specific preferences in adult male-female interactions (Numan and Young, 2016). Thus, an animal's mating and social system has a considerable impact on the influence and functionality of neuropeptides, which in turn influence brain activity and behavior. Natural selection likely drives the dramatic shifts in the differing propensity to form and maintain certain relationships observed between species.

Within the primate order, the diversity of social and mating systems results in a broad array of social relationships, between and within species (Cheney and Seyfarth, 2008). Chacma baboons, for example, have enduring mother-daughter bonds, dominance relationships, short-term sexual consortships and male-female 'friendships' to protect offspring from potential infanticide. Playback studies have shown that these relationships are not only evident to humans but are also highly salient to the baboons, such that baboons monitor each of these relationships in other baboons (Bergman et al., 2003; Crockford et al., 2007; Cheney and Seyfarth, 2008). Strikingly, one individual can be party to all of these relationships simultaneously, and actively engage in each type of relationship within minutes of each other. An adult female can be simultaneously a mother, a daughter, hold a position within the dominance hierarchy and be on a sexual consortship. We will examine what is known about how hormones interact to facilitate or impede different social relationships and social interactions.

A key theory for explaining oxytocin involvement in different affiliative relationships is that neuroendocrine circuitry which facilitates the formation of mother-offspring bonds has been co-opted to support other relationships, such as pair bonds, adult platonic friendships and

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