

Neuropeptides influence expression of and capacity to form social bonds

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Abstract: In the present commentary we expand on two concepts relevant to understanding affiliative bonding. Differences and similarities between the functions and actions of oxytocin and vasopressin are difficult to study but may be critical to an understanding of mechanisms for social bonding. What is termed here a “trait of affiliation” may reflect in part the capacity of these same peptides to program the developing nervous system.

As is well-documented by Depue & Morrone-Strupinsky (D&M-S), the concept of affiliative bonding has acquired diverse meanings, ranging from neuroendocrine-based behavioral processes, measured by selective social behaviors, to individual differences and personality traits, which in turn may influence all aspects of social behavior. Recent neuroendocrine research using animal models (Carter et al. 1995) has revealed that both the immediate and long-lasting effects of social experience on the tendency to form social bonds are mediated, in part, by two ancient neuropeptides, oxytocin and vasopressin.

If we are to understand the biological basis of affiliative behaviors, a deeper understanding of the actions and interactions of oxytocin and vasopressin will be needed. For example, among the short-term processes affected by these neuropeptides are approach behaviors and appropriate reactions to novelty that are necessary to permit interactions with a social partner. Social recognition (Winslow & Insel 2004) and social engagement (Porges 2003a) are initial steps in social behavior and required for social bond formation; both are affected by oxytocin and vasopressin. Oxytocin, acting on various substrates including the hypothalamic-pituitary-adrenal (HPA) axis and sympathetic nervous system, can be a powerful anxiolytic agent, capable of modulating reactions toward either novel adults or infants (Carter 1998). Moderate levels of vasopressin also may be anxiolytic, but it is possible that at higher doses or through effects on different tissues – for example, peripheral baroreceptors – vasopressin may have different behavioral effects. In addition, a voluntary immobilization without fear may be a feature of affiliative behaviors including lordosis or kyphosis. The ability to immobilize without eliciting autonomic reflexes (such as syncope) can be facilitated by oxytocin (Porges 1998; 2003b). However, centrally active vasopressin, although capable of facilitating affiliative responses (Cho et al. 1999; Lim et al. 2004a; 2004b; Winslow et al. 1993), is generally associated with mobility and the activation of the sympathoadrenal systems that support motor behavior. Furthermore, because portions of the vasopressin system are androgen-dependent and some aspects of oxytocin’s functions are estrogen-dependent, knowledge of oxytocin and vasopressin has begun to suggest insight into the expression of sociality and into the nature of sex differences in social behavior and social bond formation (Carter et al. 1995; DeVries et al. 1996). Thus, it is unlikely that these two peptides have identical effects on either the organization or expression of social behaviors, but their differential properties remain poorly understood.

D&M-S have emphasized the “trait of affiliation.” Genetic differences are one source of variance in sociality (Lim et al. 2004a). But genetic differences are not sufficient to explain the individual variations in social behaviors that have been observed even in presumably simple organisms like voles (Roberts et al. 1998). There is increasing evidence that social experiences, especially in early life, may contribute to enduring changes in patterns of behavioral

responses, possibly including alterations in the capacity to exhibit social bonds (Bales & Carter 2003a; 2003b; Bales et al. 2003; 2004a) or other forms of social behavior (Levine 2001; Weaver et al. 2004). For example, when prairie voles are deliberately not disturbed during the pre-weaning period, subsequent tendencies to be either social or exploratory are reduced (Bales et al. 2003).

Remarkably, during early development the same peptides that are implicated in adult social behaviors appear to be capable of programming individual differences in sociality (Carter 2003). The capacity of these neuroendocrine systems to undergo long-lasting functional modifications presents an epigenetic model that may help to explain the origins of traits that have been called personality or temperament, or by D&M-S, those termed “affiliation traits.”

In prairie voles exposure to exogenous oxytocin during neonatal life has the capacity to facilitate a later tendency to form pair bonds (Bales & Carter 2003a), may reduce behavioral and neuroendocrine reactivity to a novel environment (Bales & Carter, unpublished data), and enhances subsequent hypothalamic synthesis of oxytocin (Yamamoto et al. 2004). In contrast, even brief neonatal exposure to an oxytocin receptor antagonist (OTA) may disrupt subsequent social behaviors, including the tendency to form social bonds, to exhibit parental behaviors, and to manage anxiety or stress. Many of the consequences of early peptide manipulations are sexually dimorphic and map to sex differences in behavior. Ongoing research (Bales et al. 2004b) has revealed that a single exposure to an OTA on the first day of life produces a long-lasting reduction in vasopressin (V1a) receptor binding in the extended amygdala and reductions in vasopressin synthesis in the paraventricular nucleus (Yamamoto et al. 2004) in males, but not in females. The androgen-dependence of hypothalamic vasopressin and the sexually dimorphic capacity of an OTA to down regulate both vasopressin receptors and vasopressin may help to explain the fact that OTA exposure was especially disruptive to male behavior. In contrast, in females, but not males, a single treatment with exogenous oxytocin produced reductions in V1a receptor binding in the lateral septum, medial preoptic area, and ventral pallidum. In males, early oxytocin exposure upregulated V1a receptors in the ventral pallidum. These changes in receptor binding are consistent with behavioral changes seen in these animals. There are also recent data relating the effects of vasopressin in the ventral pallidum to an increased tendency to form pair bonds (Lim et al. 2004b).

In contrast, postnatal exposure to either vasopressin or a vasopressin antagonist did not disrupt the capacity of prairie voles to pair bond. However, animals exposed to neonatal vasopressin, especially males, tended to become more aggressive, whereas aggression was very low in animals exposed prenatally to either control treatments or a vasopressin antagonist (Stribley & Carter 1999).

Taken together, these and other related findings (reviewed in Carter 1998; Carter & Keverne 2002) support the general hypothesis that social bonding is regulated in a species-dependent manner by both oxytocin and vasopressin in adulthood and also during development. Social experiences including those between adult and offspring, as well as between adults, are, in turn, mediated in part by long-lasting changes in neural systems that incorporate oxytocin and vasopressin. Adaptive changes in these systems, especially at the level of various peptides and relevant receptors, may help to explain individual differences in behavior.

The degree to which these findings might generalize to human behavior is not known. However, there is growing evidence that early experiences, including physiological and behavioral changes associated with pregnancy, birth, lactation, and the management of infants during the postpartum period have the capacity to produce long-lasting changes in behavior. Routine endocrine manipulations, including the use of exogenous oxytocin during labor and more recently the use of oxytocin antagonists, also hold the potential to influence the parent and offspring in ways that have not been investigated in humans. Even apparently simple decisions,

such as the amount of time that an infant is touched or receives other forms of social stimulation, hold the potential to retune the nervous system (Levine 2001; Weaver et al. 2004). For both practical and theoretical reasons, it is important to realize that the mechanisms underlying traits, such as capacity to form affiliative bonds, are dynamic and capable of being influenced by early experience, often through effects on the same systems that regulate sociality in adulthood.

The role of trait affiliation in human community

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Abstract: This commentary speaks to the relationship between Depue & Marrone-Strupinsky's (D&M-S's) concept of trait affiliation and affiliative memory and the formation of human community, especially among peer groups. The target article suggests a model for how and why dynamic communities form in a number of disparate contexts and under a number of circumstances.

The target article has important implications for thinking about sociability and the role of human community in both ontological human development and human evolution. There are two general ways in which Darwin's (1860) ideas of species development have been applied to the human condition. First, there is the idea that individual action and the particular genetic structure that underlie phenotype abilities are the driving force in species group maintenance and adaptability (so that the individual with the greatest phenotypic abilities has the genetic structure most valuable to the community). The human community is secondary and is dependent on the individual. This general perspective served as the basis for the eugenics movement in the early part of the 20th century and for a good deal of recent sociobiology theorizing (Dawkins 1976). The second way in which Darwin's theory has been applied is to place community at the forefront. The great adaptation of the human species is the ability to come together in communities and to employ specific qualities such as planning and coordination to solve problems that cannot be solved by separate individuals. Species-wide qualities nurtured by the community are more important than transient, individual genotype-based abilities. This second Darwinian perspective, centering on issues of sociability and mutual aid, was first introduced by the evolutionary theorist Petr Kropotkin (1902). It was also a perspective adopted by the Pragmatic movement in the early part of the 20th century (Mead 1956), and it has served as the basis for some recent sociobiology theories (Sober & Wilson 1998). We believe the Depue & Marrone-Strupinsky (D&M-S) article may help tip the balance in favor of the second, more community-oriented perspective.

First, we start where we disagree with the target article – that is, with the differentiation made between affiliation and sociability. The authors suggest that affiliation focuses on quality of relationships whereas sociability focuses on quantity. So, sociability is affected by human traits such as extraversion that have little or no correlation with affiliation. But Kropotkin's original conception of sociability stressed interaction that was based not on quality or quantity but on context (e.g., a specific situation or problem facing the species community). We believe that the authors' thesis of a two-step process of affiliation has more to offer than does Kropotkin's conception of sociability. Certain types of human interactions tend to draw humans together, with the process being both biological and historical. The authors point to a critical connection between the biological urge to engage in affiliative action

and individual human history, which helps explain how and why communities are formed through the process of sociability, and how this helps create the key human trait of identity (i.e., when affiliation merges with history, you are left with identity). This can have both positive and negative effects on the human condition. The authors allude to the idea that affiliation is neutral; that is, it is a quality that can lead to constructive human engagement (the reason it developed as a species-wide trait) but one that can also, dependent on the mixing of histories and the ecological circumstances, lead to destructive human interactions. The key is that humans are drawn together to form a community by traits that function in a prerational manner. Although it is rational that humans have greater adaptive abilities when acting together than when acting alone, this type of conscious decision-making rarely enters into initial community building. The direction the community takes after it comes together is based on a complex interaction of this prerational activity and the way it interacts with social history.

The target article suggests answers to two critical questions: why humans are drawn to each other, and why this occurs in a number of surprising, and even dangerous (for the individual) ecological circumstances. The authors suggest a two-step process to trait affiliation. The first step is when dopamine is released in the brain, whetting the human appetite for further, more intimate contact. This contact, when achieved, leads to intense gratification through the release of endorphins. There are any number of cues that can lead to the release of dopamine. Whatever the cues, once the second step reaches its apogee, the cues (may) become part of the individual's affiliative memory through suggesting the same type of gratification in future interactions. The cues that individuals are presented with, the possibility of a successful second step leading to gratification, will have long-term impact (perhaps lifelong) on the activities of the individual. What we find especially salient in this explanation for human development is that many of the cues suggested by the authors, as well as the possibility for gratification, are found in the peer group (e.g., flirtation, shared vernacular, intimate gesture). This is important for two reasons: Early communities are most easily created by those who share characteristics and aspects of identity, and the experiences in these early communities have an oversized impact on the communities individuals will be attracted to later in life because they serve as the baseline for affiliative memory. This is an important part of the group socialization theory championed by Harris (1995); that is, we are drawn to the early peer group and the microcommunity it represents and, in turn, our interactions in that peer group modify the psychological characteristics with which we are born. Thus, our genetic predispositions and our early affiliative experiences with the peer group regulate what communities we can be part of, and the role we play in them, throughout our lifetime.

Research shows that individuals are continuously drawn into communities of peers in a variety of circumstance (McPhail & Wohlstein 1983). A recent study (Buettner 2004) exploring celebratory riots suggests that amorphous dynamic communities form on the basis of some possible but unknown gratification – a possibility formed as a result of affiliative memory, as individuals recognize cues based on previous experience with peer groups. The potential for affiliating with peers overrides threats of potential harm and even punishment.

What we believe D&M-S show is that biological response to social cues is at least as important as cognitive response to social cues. The individual is not always trying to figure out what actions are to his or her own advantage, but is often drawn to community as a necessity. This can be positive, as when communities work together to solve a problem, or it can be negative, as when communities form to achieve some unknown and impossible gratification for its members. What is critical to consider in both situations is that human beings are constantly sending out and reading cues meant to draw us together. D&M-S give us a framework for understanding this process.