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Review

The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms

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ARTICLE INFO	A B S T R A C T
Keywords: Touch Social grooming Endorphins Oxytocin Social bonding Primates	Grooming is a widespread activity throughout the animal kingdom, but in primates (including humans) social grooming, or allo-grooming (the grooming of others), plays a particularly important role in social bonding which, in turn, has a major impact on an individual's lifetime reproductive fitness. New evidence from comparative brain analyses suggests that primates have social relationships of a qualitatively different kind to those found in other animal species, and I suggest that, in primates, social grooming has acquired a new function of supporting these. I review the evidence for a neuropeptide basis for social bonding, and draw attention to the fact that the neuroendrocrine pathways involved are quite unresolved. Despite recent claims for the central importance of oxytocin, there is equally good, but invariably ignored, evidence for a role for endorphins. I suggest that these two neuropeptide families may play different roles in the processes of social bonding in primates and non-primates, and that more experimental work will be needed to tease them apart.

Contents

Grooming is a major feature of primate social life, and some species devote as much as 20% of their total daytime to this one activity (Dunbar, 1991; Lehmann et al., 2007). Conventional wisdom has always assumed that this activity is solely concerned with hygiene (the removal of parasites or vegetation debris from the fur). In practice, wild primates do not suffer as much as one might expect from external parasites (these tend to be associated more often with a sedentary lifestyle based on regularly used dens). In addition, the amount of time devoted to social grooming in primates far exceeds that minimally required to keep the fur clean.

I shall argue, instead, that for primates grooming is a social activity whose function seems to be associated mainly with social

* Tel.: +44 1865 274704. E-mail address: robin.dunbar@anthro.ox.ac.uk. bonding. Bonding is a particularly characteristic feature of anthropoid primate life. Relationships of the same kind of intensity and persistence are found in most other animal taxa only in monogamous mating systems (Shultz and Dunbar, 2007). It seems that, in anthropoid primates (i.e. monkeys and apes), within-sex relationships share many of the behavioural and psychological characteristics of sexual relationships in monogamous pairs: they involve a great deal of coordination, behavioural synchronisation and compromise, and are therefore cognitively demanding. In primates, social grooming seems to play a role in facilitating these relationships by providing a psychopharmacological environment that enhances commitment to the relationship, thereby making these behavioural outcomes possible.

While all primates devote a small but significant amount of time to self-grooming, whose function is very obviously hygienic, they also devote an often very considerable amount of time to grooming other individuals. Such a massive investment in what



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seems, on face value, to be a trivial activity begs a major evolutionary question. Natural selection is an efficient process that does not often tolerate excessive amounts of slack in the biological system. Thus, the fact that such a high proportion of an animal's day can be devoted to grooming others suggests that there is a substantial benefit to be gained from doing so. Indeed, in the conventional economics of evolutionary biology, one might expect the benefit to be proportional to its cost, and that cost will usually reflect the extent to which the animal could devote that time to feeding, which could in turn be converted into additional offspring (conventionally known in economics as the opportunity cost, or regret).

It is important, in this context, to draw a very clear distinction between social grooming and self-grooming. Almost all animals self-groom, but social grooming, or allo-grooming (the grooming of another individual), is less common outside the primates. Although many non-primate taxa (notably equids, some bats, many rodents and birds, and even occasionally ants and bees) do allo-groom (or allopreen), this rarely has the intensity or involves the time commitment that it does in primates. In many of the more social bird species, allopreening is often directed at parts of the body (head and neck) that are difficult to self-preen, and is primarily thought to have a strictly hygienic function (Brooke, 1985; Harrison, 1965). Green woodhoopoe are somewhat exceptional in that they exhibit a great deal of allopreening directed at parts of the body that the recipient could itself preen, and, as in primates, this is thought to be mainly social in function since it involves the same quantitative relationship with social group size (Radford and Du Plessis, 2008). However, even in this species, allopreening of the head/neck region (those difficult for an individual to access) is more than twice as common as allopreening of all other body parts put together; moreover, allopreening of the body/wings is highly seasonal and at best occurs at a rate of one (short) bout every 3 h or so when the birds are active (Radford and Du Plessis, 2008), whereas social grooming in anthropoid primates can occupy 10-20% of the waking day.

In this paper, I first review some of the evidence for these functional aspects of primate social grooming, and then relate this to the wider question of touch in humans. I will then summarise recent developments in comparative brain evolution and suggest that these unique aspects of primate social grooming may be related to a phase shift in social style that places primates in contrast to almost all other species of vertebrates. Finally, I consider the psychopharmacological mechanisms involved, with particular attention to the roles of endorphins and oxytocin.

1. What is grooming for?

Grooming, in primates as in most species, is all about physical touch. The actions are typically bimanual, involving sweeps with one hand interspersed with plucking movements by the other (Sparks, 1967). The plucking movements are directed at skin debris (scabs, skin flakes), spots, blemishes, and the occasional ectoparasite such as a tick or leech, or at vegetation caught in the fur. These movements have two particular characteristics: they are very rhythmic, and the plucking often involves pinching and pulling of the skin that can at times be guite painful (from personal experience of being groomed by monkeys). Grooming is especially dependent on a "finger-and-thumb" precision grip that is unique to the anthropoid primates. Infant monkeys and apes are poor groomers until the pincer grip has developed properly after myelinisation has been completed at 6-8 months of age (Altmann, 1980). Moreover, manual grooming of the kind so characteristic of monkeys and apes is much less common even among the prosimian (Strepsirrhine) primates, whose pincer grip is much



Fig. 1. Frequency distribution of the percentage of total daytime devoted to social grooming by Old World primates. Data are species averages (individual groups may devote more time to grooming) and the *y*-axis indexes the number of species with a particular mean grooming time. Data source: Lehmann et al. (2007).

less efficient. Many prosimians possess a dental "comb" (a specially adapted lower incisor row) that is instead used extensively in both self- and social grooming.

The "soft" touches that arise from the gentler sweeping movements common during grooming may activate a class of slow unmyelinated CT-afferent fibres that project to both the limbic system and the orbitofrontal cortex (Francis et al., 1999; Olausson et al., 2002). This route is quite distinct from the more conventional somatosensory routes (touch, pain, heat and itch) that underpin discriminative touch sensation and involve low threshold mechanoreceptors in the skin and fast, large diameter Abeta afferents projecting to the sensory cortex; instead, the CTafferents appear to give rise to a pleasant sensation of light touch when skin is stroked lightly (McGlone et al., 2007). However, grooming by primates can also be quite rough, the effect being not unlike that of massage: it is initially mildly painful but then gradually becomes pleasant. The exact neurological processes involved in grooming are thus at present unresolved.

While it is certainly the case that animals which are groomed regularly have much cleaner fur, it is clear that grooming is more than merely a hygienic activity for primates. First, the amount of time that species devote to grooming far exceeds that minimally required for keeping the fur and skin healthy. Fig. 1 indicates the range of variation in average time spent grooming across Old World primate species. Some species devote, on average, less than 0.1% of their time to social grooming, whereas others devote as much as 17% (a nearly 200-fold difference). Note that these figures are species *averages*: individual groups within a species may devote more time than this to social grooming. The extreme case is represented by gelada: the species devotes an average of 17% of its time to grooming, but in one large social group animals devoted 20% of their time to social grooming—the largest single investment of any primate species.

By comparison, social grooming, even though widespread, seldom accounts for such lengthy time investment in non-primate species. However, it is difficult to find comparative data on nonprimate species because researchers tend to combine allogrooming with auto-grooming in a single behavioural category,



Fig. 2. Distribution of the percentage of daytime devoted to social grooming by individual species of Old World primates (prosimians, monkeys and apes) as a function of skin surface area (indexed as body mass raised to the 0.67 power). Source: data from Lehmann et al. (2007).

and even this is combined with other inactive behavioural states into a single category "rest" (perhaps itself a reflection of how little time is actually devoted to social grooming). Nonetheless, I estimate that green woodhoopoes, one of the most social allopreeners among the birds, devote only about 0.01% of their waking day to social allopreening (based on the figures given by Radford and Du Plessis (2008), allowing a generous 30 s per bout). This is a full order of magnitude less than the least social primates.

If some primate species can maintain fur hygiene with less than 1% of their time being devoted to social grooming, why should others need to spend so much? One could argue that some species are just exceptionally inefficient groomers. This might seem plausible, since some of primates (e.g. colobines and gibbons) have only vestigial thumbs and thus have some difficulty in managing the precision finger-and-thumb pincer grip that is a crucial component of the grooming action. However, most of these "thumbless" species are not especially prolific groomers: none devotes more than 6% of their time to social grooming (i.e. they lie very much in the lower half of the distribution for the primates as a whole). Nonetheless, the fact that they are manually challenged does not seem to disadvantage them, or force them to devote disproportionately more time to grooming in compensation.

More importantly, however, time devoted to social grooming does not correlate with body mass: if grooming was purely hygienic in function, then it ought to correlate with surface area (i.e. the two-thirds power of body mass), but it does not (Fig. 2). In any case, primates are able to remove a great deal of debris that inevitably clutters their fur for themselves: they do not necessarily require the assistance of other individuals to do so, other than for those parts of the body that are difficult to reach (head, neck and back) (Fig. 3). Discounting the outlier in Fig. 3 (the tail, a body part easily accessible to both self and others), there is a significant negative correlation ($r_s = -0.880$, p = 0.004) between the amounts of self- and allo-grooming that a body part receives, a finding confirmed on a wider sample of five other species of primates by Barton (1985). One might infer, on this basis, that grooming represents a reciprocal trade-off between two regular grooming partners to deal with each other's "less accessible" bits. However, the relationship is not exclusive, and there is significant overlap in the extent to which easily accessible body parts are self-groomed and difficult-to-access parts are socially groomed. More importantly, perhaps, the time given to social grooming usually far



Fig. 3. Proportional distribution of time with which different parts of the body were groomed by other individuals (allo-grooming) plotted against the proportional distribution of self-grooming. The plotted value is the proportion of all social (or all self-) grooming that is devoted to a given body part. Solid symbols are areas that are easily accessible to the animal for self-grooming (left to right: upper arm, upper leg, lower leg, lower arm); open symbols those that are difficult or impossible for it to access (left to right: back, head, chest, rump). The data are for rhesus macaques. Source: Boccia (1983).

exceeds that devoted to self-grooming, at least in the more social species. This is true not only of the total proportion of daytime allocated to each activity, but also to individual bout lengths as well: self-grooming is often relatively perfunctory.

In short, self-grooming probably is about hygiene and only hygiene, whereas social grooming seems to have more to do with relationships. The principal evidence to support that claim comes from two facts. One is that social grooming time correlates strongly with social group size (Fig. 4), a finding that has also been replicated for allopreening in birds (Radford and Du Plessis, 2008). Second, grooming is far from random within social groups: grooming partnerships tend to be consistent as well as persistent through time. At least among females, core grooming partnerships remain quite stable and do not often change frequently (in some cases, even on the scale of years); in many cases, they are matrilinearly based. Grooming partnerships are intensely social relationships.



Fig. 4. Mean percentage of available daytime spent in social grooming plotted against mean social group size for individual species of Old World primates (prosimians, monkeys and apes). Source: data from Lehmann et al. (2007).

Relationships established by social grooming have lifelong consequences for anthropoid primates. Three sets of observations on the behaviour of adult female baboons illustrate this. Among wild gelada baboons (Theropithecus gelada), the likelihood of a female going to the aid of another female when the latter is under attack is significantly correlated with the amount of time the two of them spend grooming with each other (Dunbar, 1980). In other words, grooming relationships provide a basis for alliances. Second, the reproductive success (indexed as the number of surviving infants produced) of wild female savannah baboons (Papio hamadryas cynocephalus) is correlated with the number and intensity of their relationships (which, of course, are established and serviced by grooming) (Silk et al., 2003). Although it is not clear how this effect is brought about, in all likelihood it is the protective effect that known relationships have: more dominant animals are less likely to attack or harass an individual who is known to have grooming partners who might come to its aid (Datta, 1983). Finally, female gelada seem to view their relationships as being so important that they endeavour to buffer them against time budget constraints created by the nutrient demands of growing infants. As infants grow, they require the mother to invest more heavily in lactation, which in turn means that the mothers have to feed more to fuel milk production (Altmann, 1980); however, it seems that the mothers take the additional feeding time they need to do this out of resting time initially, and conserve their social time for as long as they possibly can (Dunbar and Dunbar, 1988).

Although we have tended to de-emphasise the role of touch in our own species in favour of language-based communication, there is ample evidence that physical touch (and social grooming) still plays an important role in everyday human relationships. We still do a great deal of close contact touch, though it tends to take the form of patting, petting and cuddling. Such behaviour is, of course, usually confined to more intimate relationships, much as it is in primates. Indeed, even self-grooming in humans shares many characteristics with its equivalent in other mammals: Young and Thiessen (1991), for instance, noted that washing, drying and (to a lesser extent) anointing behaviour in humans follow a very consistent sequence (a cephalocaudal progression) that is similar to that seen in self-grooming among rodents. More importantly, humans still engage in what is to all intents and purposes genuine primate social grooming: women, in particular, often devote a great deal of time when in contact with their children (and sometimes adult partners) to fiddling with their hair, or even attending to spots and scabs and other blemishes. Although hair care has been professionalized in modern societies, it is still nonetheless a very personal thing, and many women prefer to use the same hairdresser all the time. In traditional cultures, such as the !Kung San hunter-gatherers of southern Africa, women form very distinct hair care cliques who exclusively plait each other's hair (Sugawara, 1984). In fact, it seems that physical touch has emotional and social connotations that often far outweigh anything that can be expressed in language (Burgoon, 1991; Burgoon et al., 1992; Bottoroff, 1993; Dunbar, 2004). Touch can often convey the real meaning or intention of an interaction in a way that the accompanying speech simply cannot do. To coin a phrase, a touch is worth a thousand words.

Finally, let me turn to the (evolutionary) functional aspects of grooming. In the primate literature, there has been a tendency to interpret grooming as an exchangeable resource that is traded directly for some commodity in what amounts to a biological market (Noë, 2001). In some cases, the repayment is assumed to be reciprocated grooming (with the presumed benefit being hygiene or simply the exchange of a reward that is, in itself, pleasurable) (e.g. Roberts and Sherratt, 1998; Barrett and Henzi, 2001), while in others the reciprocated benefit is assumed to be coalitionary

support (e.g. Seyfarth and Cheney, 1984). In the first case, a animal nominally makes a direct trade of 10 min of grooming for 10 min of being groomed, but in the second it effectively offers 10 min worth of grooming in the expectation that the recipient will repay this by supporting the groomer next time it is attacked. (Note that this does not imply conscious negotiation, or even a conscious appreciation of marketplace economics: functional arguments in evolutionary biology are conventionally expressed in such terms because it makes no difference whether the processes involved are purely genetic or purely conscious.)

The first suggestion obviously runs foul of the problem I noted above, namely that primates spend far more time grooming than they actually need to for hygiene reasons alone, so why should they be interested in continuing to trade beyond the minimum necessary to ensure clean fur? By the same token, while it is now well understood that grooming triggers the release of a suite of neurohormones that act on the reward system (see below), it is difficult to see why primates should be so over-addicted to this activity for its own sake in the wild compared to all other species. The second suggestion (that grooming is traded for coalitionary support) runs into a different problem: it is hard to see how the costs and benefits of grooming could realistically be equated with the costs and benefits of coalitionary support, if only because the frequency of disputes is low compared to the frequency of grooming. Even if the risks of injury during a fight are significant, it seems unlikely that the frequencies will balance out such that there can be a direct trade-off of one benefit for the other.

A more plausible interpretation is that grooming provides the psychological underpinning for an individual's willingness to offer subsequent support (Dunbar, 1988, in press). It does this not by offering a direct exchange of benefits, but rather by creating the psychological environment that allows support itself to be traded mutually. Two individuals trade coalitionary support directly with each other, but what makes that possible is the prior grooming relationship which creates a psychological environment of trust. In other words, grooming creates a platform off which trust can be built, and I shall argue that it does this by triggering a cascade of neuroendocrines that create an internal psychological environment that facilitates this. I suggest that this is part of a dual process mechanism of social bonding that involves a cognitive component layered on top of the neuropeptide cascade designed to create and sustain social bonds. I will address the cognitive component in the next section, and the neurobiological aspects in the section that follows.

2. The social brain and the nature of primate relationships

Primates have unusually large brains for body size compared to other vertebrate groups, and over the past decade or so there has been considerable interest in why this should be. The consensus is now that the explanation lies in the complexity of primate social life. Originally proposed as the Machiavellian Intelligence Hypothesis (Byrne and Whiten, 1988), this was subsequently developed in quantitative form as the social brain hypothesis based on a demonstration that both social group and other behavioural indices of social complexity correlate with relative neocortex volume in primates (Dunbar, 1992, 1998; Dunbar and Shultz, 2007; Barton and Dunbar, 1997).

More recently, we have been able to show that this quantitative form of the social brain hypothesis (principally, a correlation between social group size and brain size) applies only to primates. In most (if not all) other higher vertebrates (birds and mammals), the social brain hypothesis takes a strictly qualitative form: in all cases tested so far (carnivores, ungulates, bats and a wide range of birds), it is species with monogamous mating systems that have disproportionately large brains (Shultz and Dunbar, 2007). The difference appears to lie in the intensely bonded relationships that are particularly characteristic of primates; in all non-primate taxa, relationships of this kind are found only in reproductive pairbonds (Shultz and Dunbar, 2007). What primates seem to have done is to take the pairbond relationship and generalized it to other group members in a form of non-reproductive relationship (now increasingly being referred to as "friendships" in the technical literature: Silk, 2002). The quantitative form that the social brain hypothesis takes in primates is then a consequence of the fact that, in contrast to pairbonds, the number of such relationships is limited only by the size of the social group (Kudo and Dunbar, 2001). This then explains why primates seem to have much more cohesive and intensely bonded social groups than most other mammals and birds.

The most likely explanation for the social brain effect is that bonded relationships are cognitively very demanding. This is likely to be because mated pairs need to coordinate and synchronise their behaviour extremely closely, and at the same time must be willing to rely on each other to fulfill their respective parts of the implicit bargain that a reproductive pair represents. This is likely to be demanding because it requires an animal to be able to factor its partner's social and ecological requirements into its own decisions about how it should behave (Dunbar, in press). Failure to do so will result in the pairbond being disrupted and mates being forced into conflict with each other, or simply drifting apart.

Among primates, there is a wide range of comparative evidence to show that a number of indices of behavioural complexity correlate with neocortex size. Across species, the use of tactical deception (Byrne and Corp, 2004), grooming clique size (Kudo and Dunbar, 2001), the regular use of coalitions (Dunbar and Shultz, 2007), the use more subtle mating strategies (Pawłowski et al., 1998) and the use of social play among juveniles (Lewis, 2001) all correlate with large relative neocortex size. In all these respects, primate relationships seem to be more complex, and qualitatively different, from those of all other birds and mammals (see also Curley and Keverne, 2005; Broad et al., 2006). This thus represents a major phase shift that potentially makes it difficult to treat sociality as being homogenous even across all the mammalian taxonomic groups.

Although the kinds of relationships found in primates clearly impose a significant cognitive demand, it is nonetheless equally clear that the cognitive dimension does not provide a complete explanation of what is involved in such relationships (Dunbar, in press). Indeed, our own experience of human relationships is that more is involved than just strategic thinking. Work on the social psychology of human friendships over the past decade or so suggests that relationships involve two independent dimensions that are usually described as "behaving close" and "feeling close" (Aron et al., 1992; Depue and Morrone-Strupinsky, 2005). Behaving close clearly accords with the suggestion that pairbonds rely on close behavioural coordination. In contrast, feeling close seems to point to something at the emotional level that is less easy to define because we ourselves often have difficulty verbalizing about it: it is something that quite literally we feel rather than cognize about (Dunbar, in press). It is in respect of this second component that grooming seems to play such a crucial role in primates.

3. The psychopharmacology of grooming

One of the striking behavioural features of grooming in those species that devote very substantial amounts of time to this activity is the fact that an animal who is being groomed can become so relaxed it can quite literally fall asleep. This seems to reflect the fact that social grooming has a number of physiological effects that include a reduction in the heart rate and a lowering of behavioural indices of stress (indexed as rates of scratching and yawning) (Goosen, 1981). Schino et al. (1988) examined the frequency with which macaques engaged in displacement acts (mainly scratching and yawning) as a function of circumstances. On the assumption that this reflects the animal's level of tension, they showed that being groomed reduces physiological tension levels. These observations suggest that, in some way, being groomed is physiologically relaxing. In contrast, self-grooming seems to be a widespread response to stress in many mammal species (e.g. rats: Homberg et al., 2002) rather than a mechanism for reducing stress.

Indeed, having grooming relationships of this kind can buffer a female against stressful challenges. In a recent field study of baboons, Wittig et al. (2008) found that during a socially stressful event (a period of instability in the male hierarchy when an immigrant male challenged for dominance, with an attendant risk of infanticide), females who responded by contracting the size of their social network (i.e. concentrated their grooming on a small number of regular grooming partners) exhibited a significantly faster reduction in glucocorticoid titres than females who did not focus their grooming on core partners. Thus, it seems likely that grooming provides females with one mechanism whereby they can enhance their sense of security, with consequent amelioration of physiological stress levels.

One explanation for these findings is that being groomed results in the release of endorphins. An association between grooming and endorphin release was demonstrated experimentally by Keverne et al. (1989) in talapoin monkeys. They showed that sub-clinical doses of morphine (2 mg/kg) resulted in a marked decrease in the frequency with which grooming was both solicited and received, and in the number of grooming partners with whom grooming was exchanged. Conversely, sub-clinical doses of the opiate-blocker naltrexone (5 mg/kg) resulted in a marked increase in the frequency with which animals solicited grooming from others. In effect, animals given opiate blockade appeared not to be able to get enough grooming, whereas those given opiates acted as if they were satiated and were disinterested in either giving or receiving grooming. Similar findings have been reported for rhesus macaques (Martel et al., 1995; Graves et al., 2002). Intriguingly, there is some evidence to suggest that the causal relationship between (social) grooming and endorphins may be reversed in non-primates (at least in the case of rats: van Ree and Niesink, 1983; Niesink and van Ree, 1989), and this may be of some significance (see below).

Endorphins, or more generally endogenous opioids, play a well understood role as part of the mechanisms of pain control (Stefano et al., 2000). Endorphins seem to be especially responsive to persistent low level muscular or psychological stress, such as that produced in humans by exercise (jogging or circuit training: Howlett et al., 1984) or emotional stress (Zacur et al., 1976). As the name "endogenous opioid" implies, this is achieved through an opiate-like effect. Psychologically, this is experienced as a mild opiate "high", a corresponding feeling of well-being, and light analgesia (Belluzzi and Stein, 1977; Nelson and Panksepp, 1998; Stefano et al., 2000). This endorphin-based pain-control mechanism has turned out to be extremely widespread among the vertebrates, having been identified not only in mammals but also in fish (Sneddon, 2003; Sneddon et al., 2003). Endorphins are also deeply involved in the regulation of the menstrual hormone system in female primates (Bowman et al., 1978; Grossman et al., 1981; Abbott et al., 1986). Nonetheless, aside from the work of Panksepp (Nelson and Panksepp, 1998) and Keverne (Curley and Keverne, 2005; Broad et al., 2006), comparatively little attention has been paid to the role that endorphins might play in regulating social behaviour. One reason for this may lies in the fact that endorphins are difficult to assay in living organisms (especially humans): unlike many other neurohormones (e.g. oxytocin), they can only be sampled in cerebrospinal fluid.

Opioids are thought to derive from fibres that arise in the arcuate nucleus of the hypothalamus and target a number of brain regions that express opiate receptors (OR), including the brainstem, basal ganglia and corticolimbic regions, as well as in hypothalamic nuclei where the neurons for other potentially important neuropeptides such as oxytocin and vasopressin (see below) are located (Stefano et al., 2000). B-Endorphin neurons, in particular, also project anteriorly from the arcuate nucleus to the dorsomedial and anterior hypothalamus, the medial preoptic area, the septum, nucleus accumbens and the stria terminalis (Strand, 1999), as well as laterally to the central, medial and basolateral nuclei of the amygdala (Herbert, 1993). As such, these areas may be well placed to receive input reflecting physical touch (perhaps through CT fibres, perhaps through other routes) and project this on to the brain's reward centres (including the medial prefrontal cortex and orbitofrontal cortex).

An alternative mechanism that has been suggested for the neuroendocrine underpinning of social bonding involves the neurohormones oxytocin (OT) and arginine vasopressin (AVP). Oxytocin and vasopressin are closely related nonapeptides that seem to play a role in the processes of pairbonding in mammals (Insel and Shapiro, 1992; Winslow et al., 1993; Williams et al., 1994; Carter et al., 1995; Insel and Hulihan, 1995; Cho et al., 1999; Young, 1999; Insel and Young, 2000). These two neuropeptides are biochemically very similar to each other: they differ by just two positions (a PHE substituted for an ILE at position 3, and an ARG for a LEU at position 8), the genes that code for them are located on the same chromosome at positions that can be as close as 15k bases apart. Moreover, the locations within the supraoptic and paraventricular nuclei of the hypothalamus that produce oxytocin (and the magnocellular neurons that convey it away from the hypothalamus to receptor sites elsewhere in the brain) lie directly adjacent to the ones that produce vasopressin (Moore and Lowry, 1998). Oxytocin is particularly heavily involved in mammalian reproduction, playing an especially crucial role in enabling the birth process and, subsequently, lactation. In contrast, vasopressin is mainly implicated in the body's control of water balance and urinary function.

Despite being present (and physiologically active in other respects) in both sexes, oxytocin and vasopressin seem to play sex-specific roles in the social domain, with oxytocin being active in females and vasopressin in males. Experimentally manipulating the density of vasopressin receptors in the ventral pallidum using viral vectors, for example, directly affects the strength of partner preference in the absence of mating in male voles (Pitkow et al., 2001; Lim et al., 2004). Similarly, Lim et al. (2004) found that it was possible to greatly increase the frequency of huddling with a partner (pairbond-like behaviour) in the normally polygamous male meadow vole by using a viral transplant of vasopressin genes into the ventral forebrain. In contrast, oxytocin seems to play this role in female voles Carter et al., 1995; Insel and Young, 2000).

In addition to this evidence suggesting a role for oxytocin/ vasopressin in the pairbonding behaviour of mammals, there is a very substantial literature linking oxytocin to mothering behaviour in mammals, including humans (Uvnäs-Moberg, 1996; Uvnäs-Moberg and Eriksson, 1996). In women, oxytocin titres following natural birth are correlated with changes in personality, including greater levels of calmness, sociability and tolerance of monotony, but not with cortisol levels (Uvnäs-Moberg et al., 1990; Nissen et al., 1998). Like the endorphins, oxytocin and vasopressin have a very wide taxonomic distribution, albeit usually in slightly different forms. In fish, these take the form of isotocin and vasotocin, respectively, while in amphibia and reptiles they appear as mesotocin and vasotocin (Insel and Young, 2000). It has been suggested that all these derive originally from a single neuropeptide widely distributed in variable form among the invertebrates, which underwent duplication early in vertebrate evolution to produce the two families as we now have them (Hoyle, 1999). This may have given rise to some key neuroanatomical differences: vasopressin receptors are especially dense in the ventral pallidum, whereas oxytocin receptors are especially abundant in the nucleus accumbens.

However, we have little real idea as to how or why these neuropeptides produce these social effects, although it is clear that, like the endorphins, oxytocin (at least) has analgesic and reward properties. In rats, high doses of oxytocin give rise to a sedativelike effect, including lowered blood pressure and reduced locomotion (Uvnäs-Moberg, 1998; Peterssen et al., 1998a,b), while the physical stimulation of suckling itself produces anti-stress effects that include a lowered blood pressure and a decreased parasympathetic tone (Uvnäs-Moberg and Eriksson, 1996; Uvnäs-Moberg, 1998) very similar to those produced by social grooming. In addition, there is some direct evidence to suggest that oxytocin may be associated with physical touch. Ågren et al. (1995) found that massage-like stroking of rats' abdomens raised plasma oxytocin levels. This was associated with enhanced tolerance of pain (as measured by latency to withdraw from heat or respond to mechanical stimulation). Similarly, in women, the reported frequency of physical contact (hugs) with partners was correlated with elevated oxytocin levels and lowered blood pressure (Light et al., 2005). Oxytocin also plays a role in ameliorating stress. Amico et al. (2004) reported that female oxytocin-deficient mice were more nervous in novel environments and had higher stress levels (indexed by corticosterone titres) in response to environmental stressors than did wild-type mice, and that these symptoms could be alleviated by injecting oxytocin directly into the cerebral ventricles.

More interestingly, vasopressin has been found to have a significant effect on aspects of social memory in male mice: vasopressin VIa receptor knockout (VIaRKO) males show a marked impairment of social (but not spatial) memory compared to wild-types (Bielsky et al., 2004). Social memory was here indexed by habituation of the olfactory investigation response to a familiar ovariectomised female, and subsequent dishabituation to a novel female. In a follow-up study, Bielsky et al. (2005) used injections of a VIaR-specific antagonist to show that vasopressin receptors in the lateral septum, but not the medial amygdala, are critical for social recognition; moreover, function could be recovered by a viral vector to induce VIaR re-expression in the lateral septum in VIaR knockouts. Conversely, over-expression of VIaR in the lateral septum of wild-type mice resulted in an increase in anxiety-like behaviours, as well as a significant improvement in social recognition. Although it is clear that vasopressin plays a significant role in regulating social behaviour in these species, it is far from clear either how this is mediated or just what this means for sociality: social recognition of potential mates is clearly important in social life, but it is not the same thing as sociality in the bonded sense we discussed above in relation to primates.

So far, all such studies have been carried out on rodents. However, Bales et al. (2007) recently used neuroimaging to show that two brain areas specifically associated with OT and AVP uptake (the nucleus accumbens and the ventral pallidum) are especially active in male titi monkeys when these are first paired with a novel female. In contrast, areas not normally associated with pairbonding (e.g. the caudate-putamen, amygdala and periaqueductal gray) showed no difference in glucose uptake between paired and unpaired males; nor were there differences in cortisol levels. However, this effect was only seen in newly paired males. Males in long-term relationships behaved more like unpaired males, and this contrast may be significant (see below).

4. Discussion

Taken together, these findings suggest that oxytocin (but not vasopressin?) might function in a similar way to endorphins in producing a sense of calmness and contentedness. However, if so, it is far from clear what the causal sequence is here, since most of the circumstances that stimulate the production of oxytocin (mating, birth, breastfeeding, stroking) all involve mechanical stress, and are thus also likely to trigger the release of endorphins. Since neuroendocrines often operate in cascades, it is far from clear just which neuropeptide is having which effect, especially since almost all studies focus on only one or other of these neuropeptides. Indeed, in addition to endorphins and oxtocyin/ vasopressin, there is evidence for possible roles for dopamine and serotonin (Depue and Morrone-Strupinsky, 2005) and perhaps even norepinephrine (Nelson and Panksepp, 1998) in these bonding processes.

Unfortunately, one of the central problems in this area has been that researchers have typically partitioned out into two nonoverlapping camps (those who favour oxytocin [\pm vasopressin] and those who favour endorphins), and so far little attempt has been made to experimentally tease apart the psycho-pharmacological effects of these two nonapeptide families (see also Depue and Morrone-Strupinsky, 2005). Recent experimental studies have revealed, for example, that nasal inhalation of oxytocin significantly enhances levels of trust and cooperation in economic games in humans (Zak et al., 2004; Kosfeld et al., 2005). However, laughter (which is an effective mechanism for stimulating endorphin release) also increases cooperation levels in these kinds of games (van Vugt et al., submitted for publication).

Another criticism of the experimental work on oxytocin and vasopressin is that it has typically tested animals only in the immediate aftermath of pair formation. The evidence suggests that the effectiveness of oxytocin (at least) wanes quite rapidly after first contact (Carter et al., 1995; Wallner et al., 2006). Since oxytocin is known both to increase rates of social contact and to stimulate grooming (Witt et al., 1992; Argioglas and Gessa, 1991), it could well be that oxytocin's role is simply to facilitate the social engagement needed to bring about the endorphin release that is actually critical to social bonding. Depue and Morrone-Strupinsky (2005), in particular, have argued for a crucial role for opioids (and in particular μ -opiates) in the maintenance (as opposed to initiation) of relationships, especially in humans.

A further issue is that all these neuropeptides (including serotonin and dopamine) are involved in the reward system; indeed, most of their receptor sites are in areas known to be part of the reward system. There has been an inevitable temptation to interpret this process as being simply one of physiological reward, and the process of social bonding thus simply as one of associative learning (e.g. Insel, 2003). However, even though animals (and humans) find activities that trigger the release of these neuro-hormones rewarding, it is far from clear that this is all that is involved. I have suggested that, even though reward provides the proximate mechanism for engaging in the appropriate social interactions, the more important function of endorphins – at least

in primates – may lie in the creation of a psychopharmacological environment in which mutual trust can develop. If the process is purely an appetitive one that achieves consummation via instantaneous pleasure, it is difficult to see why grooming partners would be willing to form coalitions that can involve serious risk of injury.

Finally, this raises the distinct possibility that the various sets of neurohormones actually play different roles in different mammalian groups. Curley and Keverne (2005); Broad et al. (2006) have suggested that there may have been a phase shift from oxytocin/vasopressin to endorphins as the core bonding mechanism during the transition from basal mammals to primates. This would accord well with the comparative brain evidence suggesting a similar qualitative shift in the nature of social relationships. It would also make sense of the fact that the effects of oxytocin and vasopressin seem to be quite short-lived, and even in rodent models to be associated with first contact rather than prolonged association. One explanation would thus be that the oxytocin/vasopressin route provides a mechanism allowing two individuals to be interested in each other. For most species, this may be sufficient to facilitate pairbonded relationships. But in primates, an additional endorphin route seems to be needed to sustain the longer term, more intense relationships characteristic of these species. If so, then a rodent model of social bonding may not necessarily help us to understand the processes of social bonding in primates in general, or humans in particular.

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