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Review article

The effect of oxytocin on human-directed social behaviour in dogs (*Canis familiaris*)

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ABSTRACT

The oxytocin system has recently received increasing attention due to its effect on complex human behaviours. In parallel to this, over the past couple of decades, the human-analogue social behaviour of dogs has been intensively studied. Combining these two lines of research (e.g. studying the relationship between dog social behaviour and the oxytocin system) is a promising new research area. The present paper reviews the existing literature on how oxytocin is related to different aspects of human-directed social behaviour in dogs.
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Contents

1. Introduction

Oxytocin – which undoubtedly plays a central role in the expression of the high levels of sociality that are essential to contemporary human behaviour (Carter, 2014) – is in evolutionary terms a remarkably conservative nonapeptide, that appears to play a particularly prominent role in the modulation of social life across mammalian taxa (Yamasue et al., 2012). However, despite the initial consensus on the prosocial effects of oxytocin, different explanations have been proposed for how these effects are mediated and the differences between viewpoints are often implicit rather than clearly delineated (Campbell, 2010). Much of the debate focuses on methodological issues about which are the low level (e.g. cellular) mechanisms behind the oxytocin effects and how results of different studies can be compared (Quintana et al., 2014). Our current knowledge of the behavioural effects of oxytocin in humans is mainly based on three mostly independent approaches: (i) correlational studies measuring oxytocin in the periphery (urine, saliva, blood) or in the Cerebro-Spinal Fluid, (ii) gene × behaviour association studies involving receptor (*OXTR*) polymorphisms, and (iii) experimental studies manipulating (both the peripheral and central) levels of oxytocin using intravenous or intranasal administration (for an evaluation of these approaches regarding their informative value in terms of the underlying central nervous mechanisms see: Heinrichs et al., 2009).

The number of published papers on dogs' (social) cognition is rapidly growing (Bensky et al., 2013) due to the fact that dogs have been proven to display human-analogue social skills (Hare and Tomasello, 2005; Miklósi and Topál, 2013). Thus, not surprisingly, researchers have also begun to study the relationship between the oxytocin system and social behaviour in the dog.

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2. The effect of dog–human social interaction on peripheral oxytocin levels

The first studies aiming to unravel the relationship between oxytocin and human-directed social behaviour in dogs tested the effect of positive social interaction on peripheral oxytocin levels (Table 1). It was found (Odendaal, 1999, 2000; Odendaal and Meintjes, 2003 — data of same subjects published with slighly different focus) that dog–human social interaction increases both dogs' and humans' blood oxytocin level (as measured by high-performance liquid chromatography technique — HPLC) compared to baseline (before interaction). Other physiological changes included increased levels of beta-endorphin, prolactin, phenylacetic acid and dopamine, as well as decreased heart rate. The social interaction in these studies consisted of a maximum 30 minute session (the intervention was finished when a stable drop of at least 5–10% in blood pressure was experienced) including softly talking to the dog, gently stroking the dog with long smooth strokes, low-key playing and scratching the body and ears of the dog. Participants (N = 18) were both owners with their private dogs and non-owners with dogs from the animal facility of the University of Pretoria. These results were conceptually replicated (Handlin et al., 2011) on N = 10 female volunteers and their own male Labrador dogs. At the end of a 3-minute-long interaction, which consisted of petting and stroking different parts of the dog's body and talking to it, an increase in blood oxytocin level was found (using immunoassay technique). Stroking the abdominal area for 15 min without social reinforcement such as vocal encouragement and eye contact by experimenters who knew the dogs well, but were neither their owners nor caregivers was also found to increase peripheral oxytocin levels as measured (using radioimmunoassay technique) from urine samples 1 h after the initiation of stimulus (Mitsui et al., 2011). In this experiment (N = 9) dogs from different breeds were tested and stroking was found to increase oxytocin levels compared to baseline similarly to other reinforcing treatments such as eating and exercising, but not drinking water. Reunion after separation from a familiar person was also found to increase blood oxytocin levels in (N = 12) laboratory-kept beagle dogs (measured with immunoassay) compared to a pre-separation baseline phase (Rehn et al., 2014). Furthermore if the familiar person made both physical and verbal contact with the dogs upon reunion oxytocin levels remained higher than baseline in the post-reunion phase as well. But this effect was not found when the dog–human interaction did not involve physical contact (verbal contact only or when ignoring the dog). Recent (unpublished) research (MacLean et al., 2017) has shown that salivary OXT levels also increase similarly to blood oxytocin levels after 10 min of free-form friendly interaction with a human experimenter (N = 19), but not after a control treatment (dog rested quietly in the same environment, without human interaction; N = 19).

These results (and others not measuring dog oxytocin levels directly) have led to the supposition that the oxytocin system plays a crucial role in dog–human interactions and serves as a potential underlying mechanism behind animal assisted therapy (Beetz et al., 2012; Pop et al., 2014). Others (Rehn and Keeling, 2016), however, have pointed out that further studies are needed in the field of dog–human relationships, potentially at the individual dog level (rather than talking about the 'average' dog), and incorporating both the owner's overall caregiving strategy and a dyadic approach. While all the above mentioned studies have been conducted on relatively low sample sizes, and have striking methodological differences (e.g. length and specifics of the interaction) and confounds (e.g. using one's own dog or another dog), taken together these findings present strong evidence that generally positive interactions with a human increase oxytocin levels in dogs. This is in line with results from other species including humans (Feldman et al., 2010; Gordon et al., 2010), rhesus macaques (Maestripieri et al., 2009; Winslow et al., 2003) and prairie voles (Kenkel et al., 2012). The relationship between positive social interaction and oxytocin increase in dogs can serve as a starting point for future research into both individual differences and different types of interactions. It has been found for example, that from the ostensive cues (eye-contact, dog-directed talk, calling the dogs name) that humans naturally use in positive social interactions (Topál et al., 2014), dogs are most sensitive to eye contact, while less sensitive to hearing their own name as opposed to a random name (Kaminski et al., 2012). It can thus be supposed that the elements used in combination during positive dog–human social interactions (eye-contact, petting, dog-directed talk, naming) are not uniformly important in modulating dogs' oxytocin response. It is also likely that the relationship between the dog and the interacting human modulates changes in oxytocin level. Dogs have been shown to behave differently towards humans depending on their familiarity and social relatedness (Horn et al., 2013; Kerepesi et al., 2014), and for example in chimpanzee the differences in relationship have been found to modulate changes in the peripheral oxytocin level after positive interactions (Crockford et al., 2013).

Investigation of individual differences has been attempted by a questionnaire-based study (Handlin et al., 2012) during which blood samples were collected from N = 10 male Labrador dogs (same subjects as in Handlin et al., 2011) and mean oxytocin levels were measured (immunoassay) during a 60-min period including a 3-min social contact with the owner at the beginning. It was found that dogs' mean oxytocin levels were related to items indicating the intensity of the dog–owner relationship (as measured by the Monash Dog Owner Relationship Scale). The study also demonstrated a positive correlation with the frequency of owners kissing their dogs and the perceived bond with the dog, and a negative correlation with the frequency of giving food treats to their dog. Higher oxytocin levels in the dogs were also associated with the owners having a perception of their dogs being less difficult to look after and less thought of as making a mess. These results can be due to both differences in baseline oxytocin levels as a function of the above psychological characteristics as well as a differential reaction to social interaction with the owner depending on their relationship. A more recent study (Pekkin et al., 2016) has also found a relationship between behavioural scales of a validated questionnaire and dogs' oxytocin levels. Specifically *General fearfulness*, *Noise fear frequency* and *Reactivity index* (derived from a set of questions about fearful reactions towards loud noises) were positively related to baseline urinary oxytocin to creatinine ratio (measured with an enzyme-linked immunosorbent assay kit) in N = 23 dogs suffering from noise phobia (the original study sample consisted of N = 28 dogs from 14 breeds, where Lagotto Romagnolo, N = 7, and Staffordshire Bullterrier, N = 6, were the most frequent breeds). These results show that, at least in this specific sample of noise phobic dogs, urinary oxytocin is not as good an indicator of positive welfare states as suggested before (Mitsui et al., 2011). These low-sample size studies, while still preliminary, suggest that focusing on individual differences in dog behaviour and their relation to oxytocin levels is a valid approach that needs attention in the future. In addition to the questionnaire survey Pekkin et al. (2016) also conducted a behavioural test where the effect of a deep pressure vest (10–12 mm Hg) versus a light pressure vest (2–3 mm Hg) and control (no vest) treatment was assessed in a simulated firework test during three two-minute intervals (pre-noise, noise, recovery) in a within subject design. Urine samples were collected at least one week prior to the test, one at baseline and one after wearing the deep vest for 30 min. The two urine samples did not differ regarding oxytocin to creatinine ratios and there was a strong positive inter-correlation. The authors also report that there were no correlations between urinary oxytocin and salivary cortisol levels; we should note, however, that saliva samples were collected on the days of the behavioural test (total of four samples before and after each test occasion), thus although no difference was found in cortisol level between treatments or test days, as the oxytocin and cortisol samples were collected on different days, the lack of correlation is not surprising). On the other hand, urinary oxytocin levels correlated positively with time spent near the owner during the recovery interval in case of the deep vest treatment. The authors also reported a

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