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Stress, security, and scent: The influence of chemical signals on the social lives of domestic cats and implications for applied settings

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ABSTRACT

Although millions of cats live among humans worldwide the scientific community knows relatively little about cat behavior and cognition. Olfaction is an important perceptual sense for many members of Carnivora, however the role of chemical signals in cat social relationships is not fully understood. Research indicates chemical signals play an important role in many areas of cat behavior including mother-offspring and conspecific interactions and exploration of their environment. Chemical cues appear to play a role in stress and anxiety reduction, allowing cats to feel secure in their environment. A better understanding of cat chemical signals, especially as it relates to within and between species communication, may lead to an increase in cat wellbeing as humans can utilize this knowledge in applied settings. Therefore, the purpose of this review is to investigate how cats process and use chemical signals in social contexts and identify ways this information can be applied to address cat behavioral issues, such as inappropriate litter box and scratching behavior, and improve cat welfare, including species-appropriate ways of reinforcing the human-cat bond.

1. Introduction

Chemical signals, which include pheromones and "signature mixtures", are an important component of communication for members of the order Carnivora and are often used to facilitate or promote species-typical behaviors (Crowell-Davis et al., 2004; Gorman and Trowbridge, 1989; Pageat and Gaultier, 2003; Wyatt, 2010). Wyatt (2015) defines pheromones as a molecule or set of chemical compounds that have evolved for communication within a species. One individual emits the pheromone, which elicits a stereotyped behavior or response in the conspecific receiving the pheromone. Animals also produce signature mixtures, which are signals with a unique chemical profile that may be used to distinguish individuals or members of a specific group. All signature mixtures, and almost all pheromones, are detected by olfactory processes in the main olfactory system or vomeronasal organ (Wyatt, 2010).

Although millions of cats, *Felis sylvestris catus,* coexist with humans worldwide, the scientific community is only beginning to understand the cognition and behavior of cats (for a review see Vitale Shreve and Udell, 2015). Chemical communication is essential for solitary cats which establish large home ranges and do not commonly encounter conspecifics face-to-face (Bradshaw and Cameron-Beaumont, 2000). These signals provide a scent history of the spatial movements, behavior, health and sexual status of conspecifics, allowing cats to gain this information without physically contacting the other individual (Gorman and Trowbridge, 1989; Leyhausen, 1965). Socially living cats engage in non-random associations with "preferred associates" (Curtis et al., 2003) and may use signature mixtures to distinguish between familiar and unfamiliar individuals (Nakabayashi et al., 2012; Natoli, 1985a) in order to engage in affiliative or agonistic interactions with these conspecifics (Bradshaw and Cameron-Beaumont, 2000; Crowell-Davis et al., 2004).

Although the production of chemical signals, their perception through olfactory processes, and the behavioral response to these signals plays a central role in domesticated cat communication and behavior (especially social behavior), the function, scope and importance of these abilities are often not given the same level of attention dedicated to other domesticated species (e.g. dogs or pigs), which may lead some to erroneously underestimate the significance of this communication modality in cats. Importantly, a better understanding of cat chemical signals has critical applied implications, as scent (and marking) plays an important role in

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many species-typical cat behaviors, problem behaviors, and can also serve as enrichment if properly understood and applied. Therefore the purpose of this review is to investigate how cats process and use chemical signals in social contexts, and identify ways this information can be used to improve cat welfare, including additional species-appropriate ways of reinforcing the human-cat bond.

2. Perception, production & behavioral response to chemical signals

2.1. Processing chemical signals

The perception of chemical cues occurs via a number of olfactory mechanisms that allow the cat to process signals they receive from other individuals. One pathway to olfactory perception occurs when a scent enters the cat's nasal pathways through their nostrils. The cat's nasal cavity is lined by the mucociliary blanket, which contains nerves, blood vessels, and cilia. The cilia aid in keeping bacteria and foreign objects out of the nasal cavity (Eldredge et al., 2008). In order to detect odor, the scent molecules must travel through the surface of the olfactory epithelium, which contains a layer of mucus, produced by the Bowman's glands and protects it from direct contact with air. After traveling through the mucus, the odor molecules reach the scent receptors, which are located on the dendrites of the first-order olfactory neurons (Bradshaw et al., 2012). Finally, signals are sent from the olfactory bulb to areas of the brain associated with the chemical structure of the odorant.

Currently, there is limited knowledge about what parts of the brain are activated in response to specific, or categories, of scents in domestic cats, although this may now be possible for future research to address given greater accessibility to brain scan technology. For example, the caudate is one region of the brain associated with processing odorants. In other species including humans, dogs, monkeys and rats (see Berns et al., 2015), a wealth of knowledge indicate activation of the caudate is associated with rewards and positive experiences. Berns et al. (2015) examined the influence of scent stimuli on the activation of brain activity in un-sedated dogs. Dogs were trained to remain still in an fMRI machine while experimenters presented scents from familiar and unfamiliar humans and conspecifics. Berns and colleagues found that although the olfactory bulb/peduncle was activated by all scents, the caudate region was maximally activated by the scent of the familiar human. This indicates dogs can discriminate the scent of individuals and they have the highest positive association with the familiar human's scent. Even though no such study has yet been conducted with cats, we propose a similar response might be seen in the caudate region of cats, which are known to discriminate between individual humans (Collard, 1967; Saito and Shinozuka, 2013; Slingerland et al., 2008), something that could be put to empirical test in the future.

The second important pathway to the perception of chemical signals in cats occurs through the mouth and involves the vomeronasal organ; a specialized olfactory organ containing neurons that detect chemical stimuli. Research on the function of the vomeronasal organ indicates it receives information from chemical stimuli, including but not limited to, sexual pheromones (Verberne and de Boer, 1976). Structurally, the vomeronasal organ is located at the roof of the mouth and is connected to the nasal and oral cavities via the nasopalatine canal (Bradshaw et al., 2012). The organ is comprised of two fluid-filled sacs that run backward from the nasopalatine canal and connect to the nasal cavity (Bradshaw et al., 2012; Eldredge et al., 2008). To process chemical cues with the vomeronasal organ, cats engage in a behavior called flehmen in which they slightly open their mouth into a grimace, allowing the ducts to open and scent molecules to pass into the vomeronasal receptors. This behavior is involved in chemosensory analysis and transports fluid-borne materials from the oral cavity to the vomeronasal organ which allows the cat to "taste" chemical stimuli (Hart and Leedy, 1987). Males engage in the flehmen behavior when identifying sexually receptive females as mates (Verberne and de Boer, 1976) and both males and females display flehmen behavior when presented with urine markings (Bradshaw et al., 2012; Hart and Leedy, 1987).

There are three families of receptor proteins within the mammalian vomeronasal organ: V1Rs, V2Rs and FPRs. Thus far, only V1Rs have been studied in domestic cats; therefore, not much is known about the functionality of the V2R and FPR receptors (Bradshaw et al., 2012; Young et al., 2010). One hypothesis is the number of V1R receptor gene variants is correlated with the ability to discriminate between chemical stimuli. Research indicates tigers have 21 gene variants (Brahmachary and Poddar-Sarkar, 2015) and domestic cats have 30 gene variants (Young et al., 2010) indicating that some felids are able to discriminate between a great variety of chemical stimuli.

Although additional behavioral research is needed to determine the extent to which cats can discriminate between scents, this research would suggest that understanding cat olfaction is just as central to ensuring optimal cat welfare as it has been considered for dogs, and could have important implications for cat enrichment. It also raises the question about whether cats could be utilized in scent based working roles in environments where dogs are less appropriate. Like other species, cats are able to discriminate between various cues, including olfactory, auditory, and visual stimuli (Burnat et al., 2005; Mayes et al., 2015; Mumma and Warren, 1968; Pisa and Agrillo, 2009; Wilkinson and Dodwell, 1980). Therefore, it may be possible to train cats for search and rescue or other scent detection applications in settings where a cat's physical agility or size would make them a superior choice (ability to climb, fit in small spaces, balance, lighter weight). More research in this area is needed for cats specifically, however similar considerations including size, weight and agility have already resulted in a broader spectrum of species being considered for use in these working roles in recent years, including the giant African pouched rat (*Cricetomys gambianus*) which has been successfully used for scent detection of landmines, tuberculosis (Poling et al., 2011; Weetjens et al., 2009) and may also prove to be a viable option for human search and rescue (La Londe et al., 2015) with additional research. Given that more cats are kept as pets in the United States than dogs, domestic cats may also prove to be appropriate alternatives for medical scent detection or olfactory assistance animals for patients who are uncomfortable with dogs or rats.

2.2. Production and use of chemical signals

Domesticated cats, like many of their wild counterparts, have a number of mechanisms to produce chemical signals. Scent glands exist throughout a cat's body, however the location and function of these glands are still debated (Spotte, 2014) Sebaceous glands are located on the head, between the digits, and in the perianal area. Temporal glands are located on each side of the forehead. The submental gland exists under the chin. The circumoral glands exist at the corners of a cat's lips (Bradshaw and Cameron-Beaumont, 2000; Crowell-Davis et al., 2004). As cats rub these glands against objects or other individuals, it is thought a secretion is left behind and the individual's scent is deposited (Crowell-Davis et al., 2004). Allorubbing, in which a cat rubs their body (often forehead, cheeks, flank or tail) against another individual, is seen as an affiliative behavior that indicates a social relationship between the individuals involved (Bradshaw et al., 2012; Crowell-Davis et al., 2004). During this "mutual rubbing" both tactile and olfactory signals are