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Review article

Olfaction in the canine cognitive and emotional processes: From behavioral and neural viewpoints to measurement possibilities

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ABSTRACT

Domestic dogs (*Canis familiaris*) have excellent olfactory processing capabilities that are utilized widely in human society e.g., working with customs, police, and army; their scent detection is also used in guarding, hunting, mold-sniffing, searching for missing people or animals, and facilitating the life of the disabled. Sniffing and searching for odors is a natural, species-typical behavior and essential for the dog's welfare. While taking advantage of this canine ability widely, we understand its foundations and implications quite poorly. We can improve animal welfare by better understanding their olfactory world. In this review, we outline the olfactory processing of dogs in the nervous system, summarize the current knowledge of scent detection and differentiation; the effect of odors on the dogs' cognitive and emotional processes and the dog-human bond; and consider the methodological advancements that could be developed further to aid in our understanding of the canine world of odors.

1. Domestic dogs live in a world of odors

Odors strongly affect the behavior of animals, thus proving important viewpoints for animal needs, experiences, emotions, and welfare (Nielsen, 2017). Chemoreception is the oldest, universal sense that preceded the evolution of specialized sensory systems (Pause, 2012), and chemical signaling is regarded as the most ancient and widespread form of communication (Bradbury and Vehrencamp, 1998). Furthermore, communicating information from one individual to another via chemosignals is also the most widely used form of communication across species: even plants (Heil and Karban, 2010) and bacteria (Taga and Bassler, 2003) rely on communication via chemosignals. For domestic dogs (*Canis familiaris*), sniffing and searching for odors is a natural, species-typical behavior and essential for the dog's welfare (Bracke and Hopster, 2006; Fraser, 2008).

Domestic dogs are one of the macrosmatic species, together with e.g., pigs and bears, meaning that they depend heavily on the sense of smell, i.e., the olfactory sense (Nielsen, 2017). Dogs live in diverse environments of smells, and with the olfactory sense, they collect information that aids in adapting to and navigating in their environment. Olfaction is

utilized in distinguishing information from the surroundings, finding the right food and mate (Nielsen, 2017), socially communicating with close-living individuals—both conspecifics (Miklosi, 2014) and non-conspecifics (Lisberg and Snowdon, 2009) and bonding with family members (Berns et al., 2015). Compared with the physical senses, such as vision and auditory senses, perhaps the greatest difference is the speed of information. Where physical senses are quick and situation-dependent, olfaction detects information from molecules, meaning that the sensory experience builds slowly, but can sustain information over time.

Olfactory perception is one of the earliest senses to develop, and it is activated before birth: dog puppies become familiarized with those odors that are introduced to their mother during pregnancy (Hepper and Wells, 2006). Detecting and learning about odors in utero is also shown in various other species, including humans (Hepper, 1995). Olfaction is believed to be the most important sense in dogs, but perhaps due to the challenges of precisely administering sufficiently small amounts of molecules in a time-locked manner, research on dog cognition has concentrated more heavily on the visual and acoustic communication of dogs with humans (MacLean et al., 2017; Molnár et al., 2009). Indeed, in

about 30,000 years of coevolution (Thalmann et al., 2013), we have become close, social partners with dogs (Udell et al., 2010), and dogs readily use visual means of communication with humans (Miklósi et al., 2003). Nevertheless, dog olfaction, and our slowly unraveling, unconscious cross-species chemosignaling with dogs, should have at least the same importance in dog social and cognitive research as visual communication (Kubinyi et al., 2007).

As humans, our sense of smell is poorly appreciated (McGann, 2017), and we don't easily recognize the importance of our olfactory sense, but we may realize its importance when its disabled. Many people noticed the importance of chemical senses during the COVID-19 outbreak, when loss of taste and smell were among the common symptoms (Han et al., 2020). We barely taste anything if we don't smell the food (Brisbois et al., 2006; Rolls, 1999). Odors are also efficiently stored in the memory, and a certain odor may bring back episodic memories from decades ago (Vermetten et al., 2007). Odors directly affect emotions, and a certain olfactory memory can evoke immediate autonomic nervous system responses, making the heartbeat faster and the palms sweat (Kadohisa, 2013; Kontaris et al., 2020). A range of effects have been reported in depressive patients, from the loss of olfactory sensitivity (Burón and Bulbena, 2013) to alterations in the pleasant sensation brought by odors (Naudin et al., 2012). In post-traumatic stress disorder patients, odors can reawaken traumatic memories (Vermetten and Bremner, 2003). As a further sign of the importance of olfaction also for humans, loss of the sense of smell (anosmia) has been associated with depression (Croy et al., 2014).

2. Olfactory processing - from the molecules to conscious experiences

2.1. Comparison of dog and human olfaction

In comparison to humans, dogs can detect significantly smaller amounts of odorants due to the high number and density of olfactory neurons, the way airflow runs in nasal cavity, and how the information is centrally processed (Alvites et al., 2023). The anatomy related to the sense of smell—for example brain areas related to smelling, such as the olfactory bulb and the olfactory cortex—are relatively large in dogs compared to those of the human body (DeLahunta and Glass, 2020;

Jensen, 2007; Sjaastad et al., 2016). Within animals of the same body mass, canids have the highest percentage of nasal epithelium devoted to olfaction, a percentage that can be linked to their enhanced olfactory ability (Sjaastad et al., 2016). Like in every other macrosmatic species, the dog's sense of smell is well developed and its importance for the dog is evident (Kokocińska-Kusiak et al., 2021).

The canine nose has some 250 million olfactory cells in addition to supporting cells and basal cells, in the olfactory epithelium which covers about 18 to 150 cm^2 (Browne et al., 2006; Sjaastad et al., 2016). In humans, the olfactory epithelium covers about 5 cm^2 and contains about 5 million olfactory cells (Sjaastad et al., 2016). Consequently, dogs trained to respond to a certain odor appear to be able to detect it at concentrations of 1000–1,000,000 times lower than humans (Alvites et al., 2023). The canine olfactory sense thus appears more sensitive than that of humans, possibly giving rise to sensations we humans do not experience (Kujala, 2017). This may be the reason why it is challenging for us humans to comprehend exactly how dogs experience their environment and how we can best co-operate with them and take their olfactory capabilities into account.

2.2. From odorant molecules to canine olfactory perception

The dog's nose is moist, which helps to capture odor molecules from the air. When a dog exhales through the slits at the sides of its nose, it creates swirls of air that help to capture odorant molecules. Fig. 1A gives an overview of the anatomy underlying the first steps of canine olfactory processing. The main parts of the olfactory system include the nasal cavity; the turbinates' that are covered with the olfactory epithelium; and the vomeronasal organ (VNO) (Jezierski et al., 2016). Odor molecules enter the nasal cavity through external nostrils. The turbinates are longitudinally folded, thin bony shelves and associated cartilage structures in nasal cavities. The anterior portions of the turbinates are covered with a mucous membrane, increasing the area lined by mucosa (Sjaastad et al., 2016). The posterior portions are the ethmoidal turbinates, and they are covered with olfactory epithelium in which the olfactory cells and their receptors are located (Sjaastad et al., 2016). The shape of the dog's skull and mouth may influence the total surface area of the turbinates and the olfactory epithelium, thus affecting the dog's olfactory capabilities (Buzek et al., 2022).
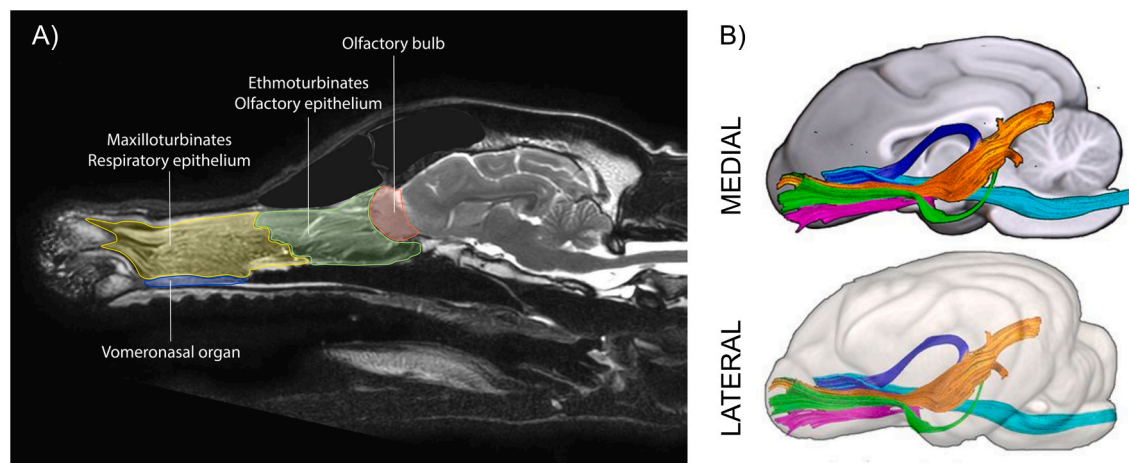

Fig. 1. A) Lateral overview of the anatomy underlying the first steps of dog odor perception. Dog nose is on the left, nasal cavity in the middle and the brain on the right. Odor molecules travel first through the nose and respiratory epithelium (yellow) towards the upper region of the nasal cavity where they are captured by olfactory receptor cells that are embedded within the olfactory mucosa in olfactory epithelium (green). The vomeronasal organ (blue), like the mucosa, is lined with epithelium tissue that contains its own separate set of receptor cells. Figure replicated under the terms of the Creative Commons Attribution 4.0 International License (CC-BY), from: Jendrny, P., Twele, F., Meller, S. et al. (2021). Canine olfactory detection and its relevance to medical detection. BMC Infect Dis 21, 838; DOI: https ://doi.org/10.1186/s12879–021-06523–8. B) Main myelinated pathways of the dog olfactory system with the different parts of the brain. Figure modified, under the terms of the Creative Commons Attribution 4.0 International License (CC-BY), from: Andrews EF, Pascalau R, Horowitz A, Lawrence GM, Johnson PJ. (2022). Extensive Connections of the Canine Olfactory Pathway Revealed by Tractography and Dissection. Journal of Neuroscience 42 (33) 6392–6407; DOI: https://doi.org/10.1523/JNEUROSCI.2355–21.2022.

The vomeronasal organ is a distinct, separate part of the olfactory epithelium, a cylindrical organ in the nasal septum and it opens into the roof of the mouth behind the upper incisors (Dzięcioł et al., 2020). Both the main olfactory and the vomeronasal organ epithelium have olfactory receptor cells, but in the vomeronasal organ, the cell membranes have stationary microvilli to increase the absorption surface, whereas the main olfactory epithelium has mobile cilia (Sjaastad et al., 2016). The main function of the vomeronasal organ is to detect molecules present in body secretions and they affect dogs' sexual behavior (Sjaastad et al., 2016). A dog must be in direct contact with the source, and they usually lick another dog's urine, drawing fluids into the vomeronasal organ. The flehmen reflex in dogs is not as typical as it is in horses, for example, but dogs also stretch head and neck forward for a short time (Buzek et al., 2022).

The olfactory epithelium consists of olfactory receptor cells (sensory cells), which are bipolar neurons (Kokocińska-Kusiak et al., 2021). When odorants reach the olfactory epithelium, the molecules activate those neurons bearing receptors for such odorants (Nielsen, 2017). A population of olfactory cells activate and generate impulses, which olfactory nerves transmit through the cribriform plate of the ethmoid bone (Sjaastad et al., 2016).

Some olfactory receptors are specialized in recognizing specific molecules, but the canine olfactory system can recognize more odors than it has specific receptors for. When a group of odorants sharing common properties reach the olfactory epithelium, the neurons that bear receptors binding to those odorants are activated (Nielsen, 2017). Those neurons that have identical olfactory receptors transmit information to glomeruli, within the olfactory bulb, which is located under the frontal lobes (Carioto, 2016). The mechanisms and full signaling cascade of the canine odor perception has been explicated in more detail recently (Kokocińska-Kusiak et al., 2021).

2.3. Olfactory processing from the nose to the brain

From the dog's olfactory bulb, olfactory signals travel to the cerebral olfactory cortex, which includes the anterior olfactory cortex, piriform cortex, peri-amygdaloid cortex and entorhinal cortex (Jia et al., 2014). Anterior olfactory cortex, piriform cortex and peri-amygdaloid cortex transmit the signals to frontal cortex and thalamus, while the entorhinal cortex transmits the impulses to hippocampal formation, where odors relate to memories (Kokocińska-Kusiak et al., 2021).

The dog's olfactory system has strong and widespread connections to different parts of the brain (Fig. 1B). Five main myelinated white matter routes from the dog's peripheral odor processing to the cortex have been recently described (Andrews et al., 2022). Notably, a large and novel tract between the olfactory bulb and occipital cortex (olfactory-occipital tract, OOT) was described, connecting olfaction with visual processing in dogs. This is the first time the connection has been found in mammals. The tract from olfactory bulb via limbic system to frontal lobe (olfactory-limbic tract, OLT) connects odorants to the brain structures involving emotion, further affecting dog behavior through the frontal lobe. The tract from olfactory bulb to brainstem (olfactory-cortico-spinal tract, OCST) connects odorants with instinctive behavior and fast behavioral responses, whereas the tract from the olfactory bulb to entorhinal cortex (olfactory-entorhinal tract, OET) connects odorants to memory formation (Andrews et al., 2022).

When a dog licks urine or vaginal secretions, the olfactory information goes to the olfactory bulb and hypothalamus via the vomeronasal organ (Sjaastad et al., 2016). The information is not transmitted to the olfactory cortex, meaning the dog is not likely to experience the sense of smell (Jensen, 2007). The main purpose for vomeronasal organ is to arouse sexual behavior by inducing secretion of hormones in the hypothalamus (Jensen, 2007; Nielsen, 2017; Sjaastad et al., 2016). Because the vomeronasal organ detects chemosignals, it also alerts the dog to various human emotional states—for example stress, anger, and happiness (Semin et al., 2019; Siniscalchi et al., 2016). Olfactory

information may also have other pathways when it does not wake conscious sense of smell (DeLahunta and Glass, 2020; Sjaastad et al., 2016). Part of these pathways goes from olfactory bulb to septal nuclei and the hypothalamus. Olfactory information can also travel through the brain network to parasympathetic motion nuclei of the brain stem, which controls odor-related reflexes and autonomic functions such as hunger and secretion of saliva (DeLahunta and Glass, 2020).

There are several factors that affect the dog's ability to smell and detect an odor: for example, environmental factors such as temperature, air pressure, humidity, compound vapor pressure and wind affect odor detection efficiency (Kokocińska-Kusiak et al., 2021; Lazarowski et al., 2020) air movement can affect odor volatility and spread, also affecting odor detection. Repeated exposure to stressful situations may affect emotions and perception of odors, especially when there is a perceived lack of control (Weiss, 1972). In addition, inflammation, alterations in blood flow and hydration, diseases (distemper, parainfluenza, or endocrine diseases: diabetes mellitus, hypothyroidism) steroids, antibiotics, and anesthetic agents have been shown to have an impact on canine scent detection (Jenkins et al., 2018). The prevalence of hyposmia in canines is unknown (Jenkins et al., 2018).

3. Contribution of odors to dog cognition

3.1. The difference of smelling and sniffing

Smelling, i.e., detecting an odor, and sniffing, i.e., actively trying to take in larger quantities of odorants, are two different processes. Smelling is unconscious, effortless, and non-cognitive process of breathing, where air has only slight contact with the olfactory epithelium, whereas sniffing is a production of short, sharp breaths at 4 to 7 Hz in dogs (Craven et al., 2009). Dogs sniff at a frequency of up to 200 times per minute (Sjaastad et al., 2016), which is ten times faster than humans (Doty, 2015). Rapid sniffing creates turbulence in the nasal passages and thereby enhances transportation of odorant molecules to the receptors in the ethmoidal cavity. Sniffing induces oscillation in the olfactory bulb, driving the piriform cortex in the temporal lobe at the frequency of sniffing (Gazit et al., 2003). During sniffing, air goes straight to the olfactory cortex through the upper flow path (Sjaastad et al., 2016). With each breath, approximately 12–13% of the inhaled air flows through the upper path and the rest flows through the lower path to the pharynx and the lungs (Craven et al., 2009). Air also uses this pathway when exhaling, but turbulence ensures prolonged exposure of inspired air to olfactory regions.

During sniffing, air is inhaled from the front and exhaled to the side and each nostril samples air separately, allowing bilateral comparison of stimulus intensity and odor source localization (Craven et al., 2009). Turbulence in nasal air flow is a consequence of anatomical and physiological factors. The ability of a detection dog to properly recognize odors relies on the humidification, warming and path of inhaled air, and guiding a portion of it towards the olfactory epithelium (Jenkins et al., 2018). Due to the large nasal cavity size, dogs have excellent capabilities of odor localization, even in the presence of background odors (Barrios et al., 2014). Thus, it is critical for the dog to sniff efficiently when searching for specific odors and locating the source (Fig. 2). A dog searching for an odor moves more slowly, and the period of sniffing lasts three times longer, during the phase when a dog is approaching its goal, compared to the initial search and tracking phases (Thesen et al., 1993). Thus, sniffing patterns in working dogs can be used to differentiate between true negative and false negative responses (Concha et al., 2014).

In practice, dogs are not able to retrieve useful olfactory information unless they sniff efficiently (Bräuer and Blasi, 2021; Thesen et al., 1993). Solely relying on passive smelling without sniffing, dogs cannot locate their owner from 18 m away (Bräuer and Blasi, 2021) thus, for dogs actively and cognitively searching for a specific odorant, sniffing is crucial. Conversely, during panting, most air passes through the mouth, thus panting evidently causes a decrease in the dog's sniffing rate (Gazit

Fig. 2. For a dog searching for a specific odor, it is critical to sniff efficiently. In nose work, the dog is ideally concentrating on the odor, ignoring external distractions. This dog is concentrating on sniffing the wall of a house, searching for a specific odor. Photo courtesy of Satu Vallenius.

et al., 2003), and olfactory efficiency (Jenkins et al., 2018). Olfactory information is processed within the canine brain in different ways. Odors can affect dog behavior through various unconscious means—meaning that the dog has no idea why it has a strong urge to behave in a certain way, e.g., to find a mate. Nevertheless, odors also affect dog cognition in multiple ways—meaning that the dog may well *know* what a certain odor is associated with, e.g. from two different scents, the dog knows which is a match for what it is searching for (Jenkins et al., 2018).

3.1.1. Scent detection and differentiation

Human utilization of canine scent detection and differentiation in a variety of tasks is one of the best-known applications of the dog's ability to cognitively process olfactory information. Due to the high sensitivity and selectivity of the canine olfactory system, and the relative ease with which dogs can be trained and handled, working dogs have been routinely used for decades as the primary means of detecting a wide range of substances in environments that contain complex background odors (Settle et al., 1994; Sommerville et al., 1993). Based on archeological evidence, the use of dogs as chemical detectors dates back far longer, to their use as hunting dogs some 12 000 years ago (Furton and Myers, 2001). Currently, dogs are the best known and widely used volatile compound detectors (Leitch et al., 2013). Humans have trained dogs to perform at least 30 different scent-related tasks (Lorenzo et al., 2003).

The most common use of detection dogs by law enforcement all over the world is for narcotics and explosives detection (Jezierski et al., 2014). Dogs are used for elimination of pests such as bed bugs (Cooper et al., 2014) and rodents (Gsell et al., 2010). They have also been used for the detection of cows in oestrus under practical conditions (Johnen et al., 2015). Dogs have also been trained to search for specific objects, such as flammable and ignitable liquid residues, guns, pipeline leaks, gold ore, and contraband food (Furton and Myers, 2001). Dogs also significantly contribute to the search and rescue of missing humans or animals, and they are used in the diagnosis of different diseases (Bijland et al., 2013). Recent studies have shown that trained dogs can even detect COVID-19 cases by smelling bodily secretions (Sakr et al., 2022), although some authors have raised concerns about their use (D'Aniello et al., 2021b). Importantly, many dogs fail training of scent detection (Maejima et al., 2007) and some have very short working careers (Evans et al., 2007). Additionally, failure in the duty of a working dog may endanger the health of both the dog and its handler (Rooney et al., 2016). Therefore, it is important to recognize and take care of the dog's welfare and minimize the disturbing effects of emotional distress.

The preceding examples point to the remarkable capability of the

dog's nose in scent-detection and it is often commented upon (Hepper, 1988; Jendrny et al., 2021). How scent detection is processed within dog cognition is remarked upon less often. Of course, the scent as such may carry a meaning for the dog—the scent of an animal a dog is actively searching for may already give a mental representation of the animal in the dog's mind—for example, that the target is a young, male dog. However, detection of the scent involves also many other phases within the dog's cognition. After the dog is trained and incentivised to mark a desired scent with a certain behavior, the dog remembers what to do when sensing the scent; and after the dog is trained to ignore all possible confusing and potentially more interesting scents, the dog uses self-inhibition and decision-making, and it is motivated to perform the task.

Training has a great effect on the dog's ability to use its skills in scent-tracking behavior (Bräuer and Belger, 2018). Trained dogs can determine the direction of a human path within five footsteps (Hepper and Wells, 2005), whereas untrained dogs are sometimes in trouble if the target odor is within a meter of them (Polgár et al., 2015). In addition, rigorous training programs lead to high frequencies of correct target alerts (Gazit and Terkel, 2003). When tracking a target, dogs appear to develop a partially olfactory representation of the tracked target (Bräuer and Blasi, 2021). In addition to the level of training causing variation, large individual differences occur in searching behavior (Bräuer and Blasi, 2021). Differences in scent-discrimination also exist between breeds (Polgár et al., 2016), and generally, German shepherds have often been superior in this kind of tasks (Jezierski et al., 2014). Therefore, detection dogs are selectively bred for olfactory capabilities and behavioral traits that are correlated with their effectiveness in the field (Prichard et al., 2020).

3.2. Social aspects of scents: knowing oneself and one's neighbors

Everyone has an individual odor; thus, it works like an identity card and scent may contribute to the definition of the self (Nielsen, 2017). While dogs are skillful at social cognitive tasks (Hare et al., 2002), communicative pointing (Miklósi et al., 2000; Miklósi et al., 1998), and even some meta-cognitive tasks (Belger and Bräuer, 2018), no evidence exists of dogs passing the mirror self-recognition task (MSR). As the sense of smell is often considered as a dogs' primary sensory modality (Berns et al., 2015; Horowitz et al., 2013), olfactory instead of visual cues could be more relevant for dogs in this task. Bekoff (2001) first noticed that a male dog spent less time in investigating its own urine than the urine of other dogs, implying that the odor of the self was, for some reason, less interesting. In the modified olfactory version of MSR, dogs investigated their own urine longer when it was modified with some other stimulus; this behavior was interpreted as implying a recognition of the odor as being of or from "themselves" (Horowitz, 2017). Nevertheless, the original developers of the MSR have provided detailed critique for these studies, suggesting that these results have not controlled for simple habituation for one's own odor, and the evidence is lacking about the connection of the odor perception with self-awareness (Gallup and Anderson, 2018). As we now know more about canine brain wiring between the olfactory and visual cortices (Andrews et al., 2022), we expect more extensive and robust studies of the canine processing of self and other in the future.

Scent processing can provide a variety of social information. Body odors in mammals constitute chemical signals that have evolved for species-specific communication (Jacob and McClintock, 2000; Wyatt, 2017, 2003). A dog can tell by the odor if an animal belongs to the same or different species; recognize if it is a prey or a predator; tell if it is immature or adult; distinguish its sex; and male dogs can also tell by the odor whether the animal is related to itself or not—possibly reflecting a mechanism to avoid inbreeding (Hamilton and Vonk, 2015). The odor also carries information about an animal's health and sickness (Nielsen, 2017). Thus, even though they are not specifically taught to discriminate between these properties, dogs can utilize a variety of social cues from

odors alone.

Interestingly, it appears that social information sensed with other modalities may also provoke cortical processing of odors. In recent studies, observing human or dog images has activated olfactory cortices in dogs (Boch et al., 2023; Karl et al., 2020). As there is a strong, myelinated connection between visual and olfactory cortices (Andrews et al., 2022), a visual social stimulus may truly elicit either a mental representation of an odor, as suggested before (Bräuer and Belger, 2018), and/or sniffing behavior in dogs.

4. Olfactory processing and canine emotional states

Psychologists describe emotional states as diverse and comprising other 'components' in addition to subjective experience, namely behavioral and physiological changes (Frijda, 1988; Lerner and Keltner, 2000; Smith and Lazarus, 1993). Emotions are also thought to result from stimulation of the nervous system, combined with the effects of hormonal inputs (Barrett et al., 2007; Kremer et al., 2020; Mauss and Robinson, 2009). The same brain structures are implicated in affective reactions for both humans and other mammals and the differences of the limbic system, the core of emotional processing, are minor (Davidson et al., 2009). Because of the differences in association cortex, humans probably experience emotions at a more conscious level than other animals, although emotions in other animals may be very similar to ours (Nielsen, 2017). Emotions are short-term reactive responses to emotion-eliciting (potentially rewarding or punishing) stimuli accompanied by physiological changes in the body, and they have biological and cognitive foundations: emotions are cognitively processed, and cognition contributes to down-regulation of emotions (Boissy et al., 2007; Damasio, 2011; Russell and Barrett, 1999). A spectrum of basic emotions can be characterized from positive to negative and on a level of high or low emotional disturbance or excitement, i.e., on a valence and arousal axes (Russell, 1980). Subjective experiences that can be characterized in terms of these valence and arousal dimensions have been labeled core affect (Russell, 2003).

Emotional–affective state plays a big role in whether the dog can achieve a task or not (Fig. 3). When examining the effects of emotions in behavior, we are facing the manifestations of emotions. Behavioral and physiological signs form the basis for the indicators of animal emotional states (Paul et al., 2005). The valence of the individual's emotional state seems to affect cognitive processes like attention, memory, and judgment (Paul et al., 2005). Emotional valence affects learning (Delgado et al., 2000) as well as memory consolidation and recall (Schwabe et al., 2012); likewise, they affect dogs' performance in detection tasks. If the dog's arousal level is low at the beginning of a task demanding inhibitory control, its task performance may increase when it is aroused (Bray et al., 2015). Conversely, if the task is carried out by dogs that start with high arousal levels, the performance of the task may decrease. Thus, when asking the dog to perform a scent detection task, it is important to consider the intensity and the type of arousal shown by the dog (Bray et al., 2015).

Odors can trigger memories and evoke strong emotions in humans, as the olfactory cortex comprises the cortical part of the amygdala (Kadohisa, 2013; Wilson and Sullivan, 2011; Yeshurun et al., 2009). As dogs have a superior sense of smell compared to humans and more widespread cortical olfactory processing networks (Andrews et al., 2022), the connection of odors to emotionality can be expected to be even stronger. The specific emotions prompted by certain odors may vary, depending on dogs' previous experiences and the physiological state of the body (DeLahunta and Glass, 2020; Sjaastad et al., 2016). However, the experimental research on the effects of olfactory processing in dogs is rather difficult and scarce, but as our knowledge of the canine olfactory world increases, our knowledge of these factors can be also expected to increase.
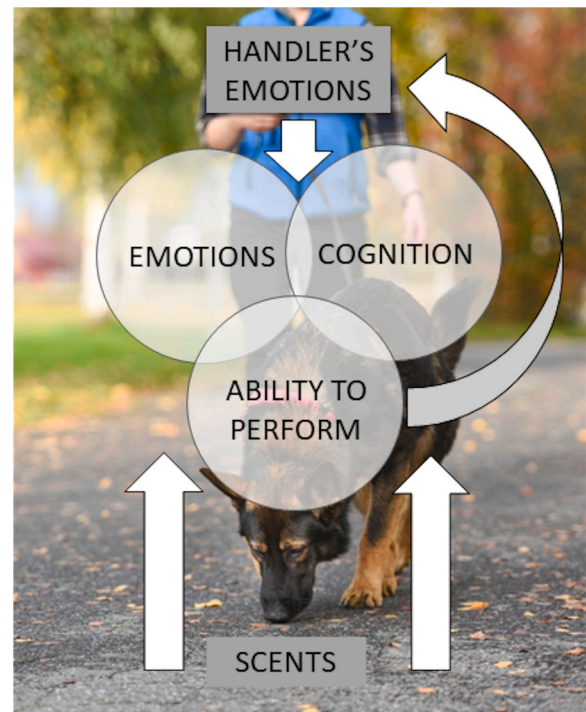

Fig. 3. Dog performance in a scent-detection task is affected by the ability to detect the scent, dog emotional state and cognitive interpretation of the situation; additionally, dog performance affect handler's emotions, which may further interact with the dog cognitive-emotional state. Photo courtesy of Hanna-Mari Laitala.

4.1. Effects of odor processing and sniffing on dog emotions

Generally, sniffing and scent work appears to increase dogs' optimism, thereby improving their welfare (Duranton and Horowitz, 2019). However, it is difficult to make conclusions on whether the dogs' state in this case a result of positive operant conditioning, when the scent work is associated with and motivated by a reward. The dopaminergic reward system appears to share anatomical similarities across mammals, and in dogs, striatum activity has been shown related to both primary rewards, such as food, and social rewards, such as praise (Cook et al., 2016). Both may be connected to the observed positive effects of scent work in dogs. The effects of reward response could be teased apart by studying spontaneous sniffing behavior of dogs, and its implications for dog emotionality.

Attempts have been made to separate the emotional valence of odors from the lateralized behavioral responses of dogs. Laterality has been noted as an ancient homologous trait in vertebrates (Miklosi, 2014), also manifested in humans within brain processing of speech production and comprehension. In a study by Siniscalchi and colleagues (Siniscalchi et al., 2011), dogs used their right and left nostrils differently depending on whether the smell was new or familiar. New odors were sniffed with the right nostril and familiar odors with the left nostril, suggesting that rewarding scents are processed in the left hemisphere of the brain and potentially threatening scents in the right.

Some studies regarding behavioral emotional responses to olfactory stimulation in dogs have been conducted. These were based on a form of sensory enrichment that involves the addition of scents or scented materials to an enclosure (Nielsen, 2017). Certain kinds of olfactory stimulation appear to have had behavioral effects in a range of contexts. Some essential oils may influence the affective states and behaviors of shelter dogs (Uccheddu et al., 2018), for example affecting activity in dogs housed in rescue shelters (Binks et al., 2018; Graham et al., 2005). Olfactory stimulation in the form of an ambient odor of lavender had a

partial relaxing effect in dogs (Wells, 2006). The synthetic version of the dog appeasing pheromone emitted by nursing females has been found to be an effective therapeutic intervention for firework phobia and travel-induced anxiety in pet dogs (Mills et al., 2006; Sheppard and Mills, 2003). Furthermore, exposure to coconut, vanilla, valerian, and ginger reduced vocalizations in the shelter dogs (Binks et al., 2018). As excessive vocalization is frequently used as an indicator of stress in dogs (Hetts et al., 1992; Stephen and Ledger, 2005; Taylor and Mills, 2007), the result may be suggestive of reduced stress in dogs after the scent has been introduced (Binks et al., 2018). Additionally, after the coconut and ginger exposure, dogs exhibited increased sleeping behavior (Binks et al., 2018). Enhanced sleeping behavior has been suggested to be indicative of relaxation and improved welfare in kenneled dogs (Brayley and Montrose, 2016; Kogan et al., 2012).

4.2. Odors in human-dog social and emotional interaction

Most of the success of dogs in our society relies on their social attention toward humans (Alterisio et al., 2019; Mongillo et al., 2015). Family dogs often initially use visual information in their communication with humans (Szetei et al., 2003) and to solve basic choice tasks (Polgár et al., 2015). However, in a long process of domestication, dogs may have also become good at dealing with interspecies chemosignalling (Payne et al., 2016; Pettersson et al., 2011). Anecdotal evidence suggests that dogs may learn to anticipate the return of the owner due to the decreasing odor concentration at home (Horowitz, 2016). Also, at least some emotional states appear to have significant chemical fingerprints that can be detected by dogs, enabling them to differentiate some human emotional states (Semin et al., 2019; Siniscalchi et al., 2016; Wilson et al., 2022).

Several studies suggest hormonal and physiological synchronization, or emotional contagion, between dog and owner. In their inaugural study, Odendaal and Meintjes (2003) showed that changes in plasma concentration of the measured neurochemicals were similar in both humans and dogs. During positive interaction, such as affectionate interaction with dogs, blood pressure decreased in both species and the hormonal levels of endorphin, oxytocin, and prolactin rose, in comparison to quiet book-reading by the owner. Oxytocin is perhaps most recognized for its role in bonding, socialization, and stress relief, and it is referred to as the "affiliation" hormone due to its role in attachment and social interaction (Miller et al., 2009; Winslow and Insel, 2002). However, human gender may affect hormonal responses to interaction with owned dogs, oxytocin appearing a better biomarker for women than men (Miller et al., 2009). Although behavioral studies may have an ensemble of uncontrolled, separate stimuli that contribute to the result—visual, auditory, and olfactory signals all mixed together—this kind of hormonal and physiological synchronization, or emotional contagion, may happen through chemosignals (de Groot et al., 2015).

In a study where dogs were remotely exposed to the sweat odor of human strangers, collected when either in a happy or fearful situation, the dogs showed different responses in the presence of the owner and an actual stranger, according to the emotional state of the other unfamiliar humans, from whom the samples had been collected (D'Aniello et al., 2018). When the dogs were exposed to the samples of happy people, they were more interested in the samples of strangers, and they showed more stranger-directed behavior; conversely, when smelling the samples of fearful people, the dogs showed more owner-directed behavior. In the fear-related odor condition, the heart rate of the dogs also increased, and they showed more stressful behavior. Similarly, clear arousal stimuli transmitted by human odors have resulted in high cardiac activity in dogs (Siniscalchi et al., 2016). These behavioral responses may indicate a form of emotional contagion mediated by chemosignals (D'Aniello et al., 2018); at least they show that dogs differentiate and respond to the emotional odors of humans in a behaviorally meaningful way.

A well-functioning human-dog bond and the scent of their owner also appears to be rewarding for dogs. When dogs were presented with five different scents during an fMRI scan (self, familiar human, strange human, familiar dog, strange dog), the olfactory bulb/penducle was activated by all scents similarly, but the caudate nucleus—associated with reward processing and positive expectations—was activated by the familiar human more than other categories (Berns et al., 2015). Although neither the human nor dog emotional state was controlled for in the study, this indicates the reward value of the mere scent of the familiar human for the dog. Interestingly for the human-dog bond, dog owners can also recognize the smell of their own pet when they are offered several odor samples (Wells and Hepper, 2000), although the reward value of the scent of one's own dog remains to be explored.

The emotional arousal and alertness level of humans and dogs appear to synchronize during a time course of a year (Höglin et al., 2021; Sundman et al., 2019). This is likely mediated by the stress-related hormone cortisol, an odorant that can be detected by dogs (Wilson et al., 2022). Different dog breeds also appear to have differential responses to human stress; herding dogs show this kind of synchronization with their owners in their cortisol levels, whereas ancient breeds do not (Höglin et al., 2021). A similar effect is suggested by the sensitivity of herding dogs to dog owner temperament: for example, detecting the stress of owners with high negative affectivity may hinder the performance of herding dogs in reading human gestures (Kujala et al., 2023). The effect of the stress-related odor may also depend on the situation: in an explosive-detection study, handler's task-irrelevant acute stress improved the dog's performance (Zubedat et al., 2014). The differentiation of human fear from happiness by dogs (D'Aniello et al., 2018; Siniscalchi et al., 2016) may also rely heavily on detecting cortisol from the odor samples. In this case, there may be differences between the dog breeds in their response to human emotions; at least differences between the sexes have been found (D'Aniello et al., 2021a). In addition, there are probably also individual differences in dogs' ability to perceive human emotion in general (Arden and Adams, 2016; Miklosi, 2014).

Dog response to human stress may also affect dog emotionality and welfare in the long run (Bombail, 2019). Repeated exposure to stressful situations affects olfactory perception, thus emotional contagion has the potential for similar effect. Chronic stress affects metabolism and the immune system, which can modify animal behavior or affect the function of olfactory epithelium; chronic stress also affects brain structures involved in emotion processing and memory formation (Bombail, 2019). Therefore, human-dog interaction and chemosignals may affect the dog's emotional behavior in a variety of ways that are not fully understood. Nevertheless, it is yet unknown whether the human-emitted odors activate automatic emotional responses or responses learned during human-dog interaction (Semin et al., 2019)—at least, even 3–6-month-old puppies exhibit behavioral responses to human fear chemosignals (D'Aniello et al., 2023). If the scents emitted during human-dog cooperation affect the work of detection dogs, it could be considered in the training. The bond and the relationship between the handler and the dog can affect the dog's arousal levels (Gácsi et al., 2013), and the handler's behavior and arousal level further affect scent detection dog performance (Zubedat et al., 2014). Indirect correlations exist between the time that military dogs spend with their handler and the dog's performance in obedience, but this has not yet been shown with scent detection dogs (Troisi et al., 2019). The dog–owner relationship and assessment of the effects of each are important areas for future research: the effect of handler arousal level and emotional state on the success of the team needs to be better disentangled (Troisi et al., 2019).

5. How to measure the effects of canine olfactory processing on cognition and emotion?

How active the animal is or how intensively it behaves can be a good measure of emotional states (Paul et al., 2005); however, the valence—whether these states are positive or negative for the animal—is crucial (Mendl et al., 2022), and it is difficult to disentangle them from

the physiological signs alone. Currently, studies with humans have been informative in estimating emotional states of animals. Predisposing animals with stimuli, which have been associated with a certain emotional state, and measuring the animals' physical responses and observing their behavior can be used as an indicator of those corresponding emotional states (Désiré et al., 2006, 2004).

5.1. Challenges in measuring olfactory processing

When studying olfactory perception, a significant problem is posed in respect of controlling and measuring quantities of odorants. Since olfactory processing is a chemical sense relying on detection of odorant molecules, its exact time course is difficult to estimate, because any odorous object releases molecules according to their vapor pressure (Lazarowski et al., 2020). Evaporation and diffusion of odorants thus varies in composition and concentration, which makes timing of perception unreliable. If the onset of the olfactory stimulus—the binding of the odorant molecule to the olfactory epithelium—is not precisely known, experimental study of olfactory perception is challenging, as conscious experiences are formed in the brain in milliseconds (Williams et al., 2004). This problem has been overcome by utilizing methodologies that do not track the exact procedure of the perception, but instead detect the long-term effects of the odorants in seconds or minutes: measuring either brain activation, autonomic nervous system reactivity, or the dog behavior related to the odor perception.

Studying olfactory processes also exhibit other challenges: a completely different kind of problem is presented by contaminants of stimulus odors. If the target odors have been handled poorly, it is possible that the dog detects contaminant and not the target (Johnen et al., 2017). Also, when examining and training dogs for scent detection tasks, the human handler may affect the outcome and interpretation of dogs' reactions. Handler skill in interpreting the behavior of the working dog is of great importance. Handlers must constantly observe the dog's sniffing intensity, respiratory patterns, and behavior. The are a multitude of things to consider when testing dogs' ability to detect scents, such as breed and individual differences, behavioral differences, training history, age, sex, health, and diet (Jenkins et al., 2018; Johnen et al., 2017; Lazarowski et al., 2020).

5.2. Indications of dog behavior as a measure of scent detection

One of the oldest and most used methods in examining dog olfactory processing is observation of tracking and quantifying behavior. For example, the behavior of animals when introduced to odors of predators has been quite well characterized (Apfelbach et al., 2005; Samuel et al., 2020; Takahashi et al., 2005). Evidence of odor sensitivity and preference can be obtained by observing animal behavior (Nielsen, 2017). Similarly, a dog's behavior can be informative on whether it detects the target odor or discriminates between two separate odors. Biologically important odors (such as sources of nutrition) have a high valence for survival; thus, they easily induce innate behavioral responses or rapid learning. Of course, interpreting dog behavior is not always straightforward, as it can be influenced by the dog's previous experience, environmental conditions, or distance to the odor source (Fig. 4). Instead of natural behavior, a more controlled approach to studying scent discrimination in dogs is teaching a specific behavior to indicate different odors or an absence of a certain odor. Using this approach, dogs can be trained for scent detection in the laboratory to aid in the diagnosis of certain diseases. In these cases, dogs discriminate, for example, between infected and uninfected urine or saliva samples detecting the unique odor signature of infected patients (Angle et al., 2016; Dehlinger et al., 2013; Essler et al., 2021; Guest et al., 2019; Hackner and Pleil, 2017; Kokocińska-Kusiak et al., 2021; Maurer et al., 2016; McCulloch et al., 2006).

Additionally, dog behavior can be used for studies of dog sensory capabilities. The dog's olfactory sensitivity has been studied by teaching
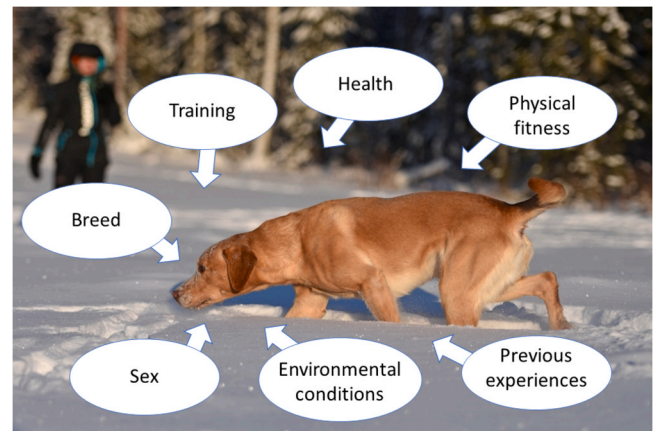

Fig. 4. Dog behavior in scent detection can be influenced, for example, by the dog sex and breed, training, health, physical fitness, previous experiences, and environmental conditions. Photo courtesy of Hanna-Mari Laitala.

dogs to respond to an odor, followed by lowering the odor concentration to the extent that dogs cease to react to it behaviorally (Krestel et al., 1984; Walker et al., 2006). To identify behavior patterns and use behaviors as alert signals for the presence of the target odor, dogs' sniffing of a carrousel arm with odor samples was videotaped and the total duration dogs spent in examining the samples; duration of sniffing episodes; and the number of attempts to sniff each of the samples was measured (Concha et al., 2014). The dogs' sniffing duration was significantly shorter when the target odor was not present and not detected (i.e., true negatives) than in false negatives, true positives, and false positives. Dogs also commonly performed two sniffing episodes when the target odor was present and only one sniffing episode when the target was not present, indicating that the clear absence of the scent is the most straightforward and induces shortest periods of examination by dogs. Similar results have been obtained using a different experimental approach, utilizing a pressure sensor measuring the potentiometer in proportion to the movement when the dog touches the plate with the odor samples (Mancini et al., 2015). The amplitude and duration of the pressure applied to the plate were lower when the target odor was not present in comparison to that of the true positive sample.

Since sniffing is important for dogs' odor detection (Laing, 1983), a simple wireless device has been developed for dogs to wear when they do off-leash searching and moving around an area (Gazit et al., 2003). This device made it possible for the handler to hear the dog sniffing or panting through radio headphones, which could be later utilized with a video footage to analyse the dog's behavior with sound recording (Gazit and Terkel, 2003). There have been efforts to replace the dog's nose with some technological methods for scent detection, yet dogs are found to be the fastest and most versatile and reliable odor detectors—the synthetic detection devices suffer from the lack of efficient odor sampling systems, poor selectivity in the presence of interfering odor chemicals limited mobility and tracking ability (Furton and Myers, 2001).

When examining dog differential behavioral responses to certain odorants, an ethogram—a well-defined record of animal behaviors—is often used in ethology. For example, in a study examining dog detection of human body odors D'Aniello et al. (2018) used an ethogram when quantifying the relevant behaviors of dogs after sniffing an odor sample: approaching, interacting, and gazing either at the owner, a stranger, or the odor sample. After grouping stress-related behaviors into an ethogram, the frequency and duration of all stressful behaviors was calculated. Similarly, dogs' behavior related to odor processing has been videotaped and studied in many paradigms: typically, the behavior duration, frequency, latency, or behavior choice may be calculated (Bräuer and Belger, 2018; Bräuer and Blasi, 2021; Siniscalchi et al., 2011).

5.3. Measuring dog physiological responses: heart rate and heart rate variability

As various emotions are linked to the activity of the autonomic nervous system (ANS) (Kreibig, 2010), physiological indicators of emotion could be informative in relation to the dog emotionality associated with odor processing (Amaya et al., 2020; Ohno et al., 2022). For example, fear and aggression lead to increased heart rate and blood pressure (Sjaastad et al., 2016). Furthermore, heart rate variability (HRV)—a measure of the variation in time between each heartbeat as controlled by the ANS—is an effective measure of the balance between sympathetic and parasympathetic nervous system (Thayer et al., 2010; Van Ravenswaaij-Arts et al., 1993). When an animal is healthy and resting, HRV is high, and in exercise, stressful situations or when an animal is sick, the variability decreases. HRV is an important bio-signal, which is utilized as an informative of the state of ANS in humans (Draghici and Taylor, 2016), cows (Hagen et al., 2005), and in dogs (Brugarolas et al., 2019; Gácsi et al., 2013; Hamada et al., 2017; Somppi et al., 2022). Several studies have used HRV in the study of emotions in dogs (Katayama et al., 2016; Maros et al., 2008; Zupan et al., 2016), although HRV markers appear reactive to both valence and intensity of emotion (Katayama et al., 2016; Somppi et al., 2022). HRV differs between breeds, being greater in brachycephalic dogs than in non-brachycephalic dogs (Doxey and Boswood, 2004). Changes in HRV in dogs have been associated with affective states such as empathy (Romero et al., 2013), anxiety (Wormald et al., 2017) and aggressiveness (Craig et al., 2017).

Although studies utilizing ANS measures in dogs exist and measurement devices have been developed (Ohno et al., 2022) there are no Gold Standards for the protocols of measuring and analyzing dog HRV, and as it is affected by many qualities often outside scientific interest—such as age, body mass, and movement (Catai et al., 2020; von Borell et al., 2007). To date, experiments regarding measurement of dogs' HRV during scent detection tasks have been at a piloting phase or the sample size has been small (Brugarolas et al., 2019; Hamada et al., 2017; Kasnesis et al., 2022; Ohno et al., 2022). Research has been hindered by measurement challenges in experimental situations—for example, movement may render the measurements difficult with Search and Rescue (SAR) dogs (Hamada et al., 2017). Therefore, examining dogs' olfactory processing with HRV measurements could be developed further to gain more distinctive information of the related emotional and cognitive processes.

5.4. Brain imaging of canine odor processing

Advances in the non-invasive brain imaging of domestic dogs offer one way for better understanding the mechanisms behind the dog's olfactory abilities as well as cognitive and emotional processing of scents. Scent detection is non-trivial as a topic of functional imaging due to its chemical nature, thus methodological advances in odorant delivery methods with precise timing have been implemented (Jia et al., 2014). Functional magnetic resonance imaging (fMRI) has shown that the odorants bind to the olfactory bulbs and affect brain processing in the piriform lobe likewise in anesthetized and awake dogs, i.e. irrespective of their state of consciousness, whereas in awake and conscious dogs, olfactory stimuli also activate regions within the frontal cortex (Fig. 5A; Jia et al., 2014). Brain imaging studies have also illustrated reward learning through response modulation in caudate nucleus after olfactory cues (Berns et al., 2015; Prichard et al., 2020, 2018) and activation of dog olfactory cortices as a response to a mere visual image of a dog body (Fig. 5B; Boch et al., 2023).

Furthermore, adding zinc nanoparticles to the odor stimulant appears to increase dog brain activation within the olfactory bulb and hippocampus (Jia et al., 2016), which agrees with the in-vitro electrophysiological data from rodents (Takeda et al., 1997; Viswaprakash et al., 2009). Although the studies in dogs are still awaiting replication, the zinc effects on brain activity suggests a possibility of better detection and memory formation of scents in dogs when the odorant stimuli have been mixed with zinc nanoparticles, apparently because zinc molecules interact with the olfactory receptor cells.

To date, the non-invasive brain studies on canine odor processing have utilized fMRI as a measurement tool. Although fMRI is an expensive method and inaccessible in many places, due to it being based-on oxygen metabolism it is temporally less precise than neurophysiological brain research methods, which require millisecond-scale temporal precision of the stimulus administration (Hari and Puce, 2023). Thus, fMRI may be better suited for localizing the brain areas responsive to odor processing, although measuring electroencephalography in canine olfactory processing may be useful in evaluating functionality of sensory processing (Hirano et al., 2000). The future perhaps awaits more studies regarding the brain oscillatory activity related with odorant processing, as brain oscillations are derived over a longer period of time and can be informative of many kinds of cognitive processing (Kahana, 2006). Nevertheless, knowledge of the olfactory system function—how the scent processing proceeds within the dog brain—is within the reach of scientific research utilizing functional brain imaging methods.
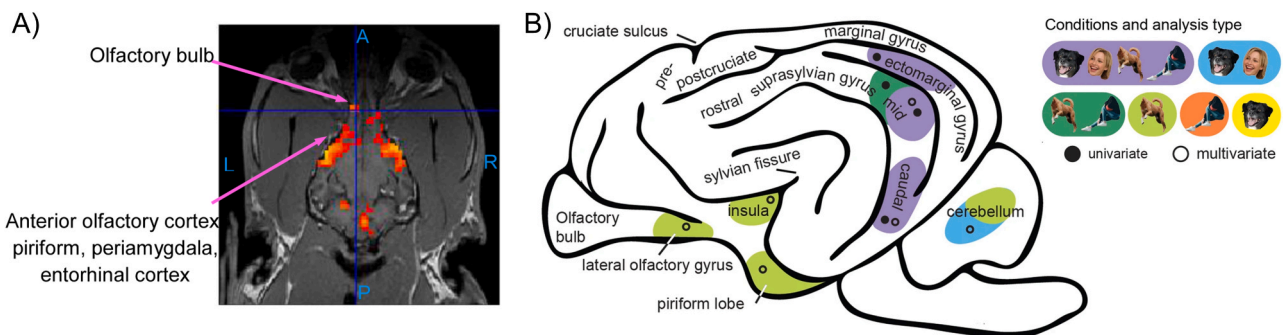

Fig. 5. A) Dog brain response to an odor, as depicted by the fMRI from the dorsal view of the head (dog's nose pointing up). Figure modified, under the terms of the Creative Commons Attribution 4.0 International License (CC-BY), from Figure 10 of: Jia H, Pustovyy OM, Waggoner P, Beyers RJ, Schumacher J, Wildey C, et al. (2014) Functional MRI of the Olfactory System in Conscious Dogs. PLoS ONE 9(1): e86362; DOI: https://doi.org/10.1371/journal.pone.0086362. B) Illustration of dog brain responsivity to different categories of visual images, depicted from the left lateral view: dog olfactory cortices were responsive to images of dog bodies. Figure modified under the terms of the Creative Commons Attribution 4.0 International License (CC-BY), from Figure 6 of: Boch, M., Wagner, I.C., Karl, S. et al. (2023). Functionally analogous body- and animacy-responsive areas are present in the dog (Canis familiaris) and human occipito-temporal lobe. Commun Biol 6, 645; DOI: https://doi.org/10.1038/s42003–023-05014–7.

5.5. Conclusions and future directions

The canine olfactory world is rich and supplies specialized information about the environment. While we do have sophisticated information of the anatomical paths and functional mechanisms of canine olfactory processing, our understanding of the meaning and representation of the olfactory stimuli for dogs is lesser. Training enables dogs to become better at differentiation of odors, but dog cognitive and affective states are reflected in the dog's behavior. Scent work may also be affected by human odors. Some measurement possibilities exist for connecting canine olfactory processing with cognition and emotion, yet they may benefit from replication, standardization, and further development. Behavior is informative about odor detection and categorization; study of brain anatomy is needed in deciphering the interconnection networks, neuronal tissue qualities and quantities; autonomic nervous system measures could fill in the gap related to the emotional provocation of scents; and functional imaging may provide information on the cognitive and emotional processes involved in the scent perception. Taking these informants together, we can derive information that may be the next best thing to subjective experience.

Declaration of Competing Interest

Authors declare no conflicts of interest

Data availability

No data was used for the research described in the article.

Acknowledgments

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