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Right nostril biases to experimental scents in *Canis familiaris*

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ABSTRACT

Although olfactory laterality in canids has been demonstrated experimentally, the extent to which nostril bias occurs in “nature” is not well known. We tested whether there was olfactory laterality of untrained dogs in various off-leash dog parks within Victoria, British Columbia to manipulated scents placed at the tail base of full-size dog replica. Using video-playback, we found that of 192 separate approaches ($N = 119$ different subjects), dogs used the right nostril first greater than 66% of the time and for longer periods when investigating estrous dog secretions, deer urine and coyote urine. Similar trends were observed when using scents on a similar-sized box rather than the dog model. There was no side preference for the scent of commercial pet food. These results support right hemisphere control of the sympathetic-hypothalamic-pituitary-adrenal axis and encourage more detailed evaluations of olfactory laterality in wild canids and other carnivores where olfaction is the major sensory modality.

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KEYWORDS Domestic dog; olfaction; laterality; nostril bias; model

Introduction

Lateralized responses to different olfactory signals have been described in several vertebrate species. In rats, odour sampling from both nostrils is highly lateralized during odour localization (Parthasarathy & Bhalla, 2013). In horses, sniffing of arousing stimuli is associated with right-nostril use coupled with increased cardiac activity (McGreevy & Rogers, 2005; Siniscalchi, Padalina, Aubé, & Quaranta, 2015). In humans, odours perceived or imagined as pleasant activated the left hemisphere more than the right (Henkin & Levy, 2001) while unpleasant smells activated the right hemisphere.

The nasal cycle in mammals is an autonomic phenomenon associated with cyclical changes in the size of the nasal passages, allowing for greater airflow and increased mucosal gland secretion in one nostril compared to the other (Friling, Nyman, & Johnson, 2014). It is thought that

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asymmetry in airflow between nostrils optimizes the perception of a given set of odorants, producing olfactory images from each nostril that are sent to the brain with each sniff (Kahana-Zweig et al., 2016).

The mammalian olfactory cortex is located within the medial temporal lobes, and transmits emotional processing from the amygdala, behavioural information from the piriform cortex and olfactory gestalts to the thalamus, which communicates with the frontal cortex, allowing for the conscious olfactory experience (Cain, 1974; Jenkins, DeChant, & Perry, 2018; Jia et al., 2014). Transmission of odour information from the olfactory receptors in the nasal cavity, through the olfactory bulb and to the olfactory cortex in the brain is largely ipsilateral, and as such, right nostril use indicates right hemisphere involvement during the neural processing of the smell with the left nostril indicating involvement of the left hemisphere (Royet & Plailly, 2004; Siniscalchi, d'Ingeo, & Quaranta, 2017).

Lateralized functional trends for olfactory investigations in the domestic dog *Canis familiaris* have been explored by Siniscalchi et al. (2011). In controlled kennel settings, dogs show an initial right nostril bias for non-aversive scents such as food or canine vaginal secretions but shift to left nostril use after repeated stimuli presentations. A right nostril bias also occurs for aversive scents such as adrenaline; however, no switch to left nostril is demonstrated after repeated exposure which supports right hemisphere dominance for the control of the sympathetic-hypothalamic-pituitary-adrenal axis (Craig, 2005; Siniscalchi et al., 2011).

We extend the research by Siniscalchi et al. (2011) and test for olfactory trends of dogs within off-leash dog parks. We placed different scents at the base of the tail of a stationary life-size dog model and video-taped at close range nostril use of approaching dogs. Scents were chosen that may be representative of prey, a competitor, a conspecific, and commercial dog food. We predicted that both heterospecific and conspecific scents would elicit an initial right nostril bias.

Methods

Recordings were collected using an SJ4000 action camera (720p resolution at 30 frames per second), made by SJCAM and analyzed using VLC media player by VideoLan. Olfactory investigations of the scent by approaching dogs were captured by mounting the camera to a life-sized black dog model (description in Leaver & Reimchen, 2008), ventrally and positioned just rostral to the hind legs, with the lens of the camera aimed caudally and angled slightly dorsally (Figure 1). While a dog model was used in our protocol as a visual stimulus to attract dogs, we also assessed olfactory trends of dogs to similar scents placed on a neutral visual stimulus, a black box (wrapped in similar black material as on the dog

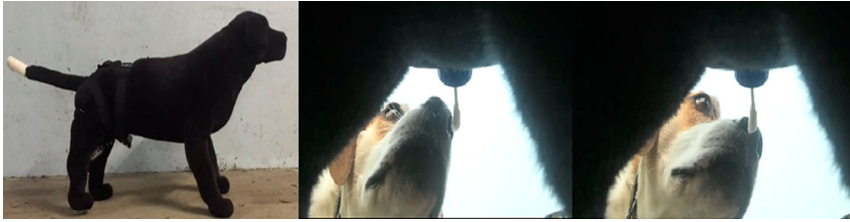


Figure 1. (Left) The dog model used for the experimental condition. (Middle and Right) Schematic representation of a left vs right nostril investigation within the experimental condition.

model) with SJ4000 action camera mounted dorsally and laterally on the median plane.

Experimental odorants were presented at a height of 28 cm on Q-tips[®] cotton swabs or surgical gauze with the same size and shape as the Q-tips[®] cotton swabs (as shown in Figure 1). Experimental odorants were; (1) urine from estrous whitetail deer (*Odocoileus virginianus*) (Tink's #69 Doe-In-Rut Buck Lure), (2) urine from coyote (*Canis latrans*) (Coyote Urine by WILDLIFE RESEARCH CENTER[®]), (3) vaginal secretion of a day 15 estrus dog (provided by a veterinarian) and (4) wet dog food (Cesar[®] Beef Stew). Each sample (1,2,4) was saturated on to a Q-tips[®] cotton swab while the estrus dog scent (3) was saturated on surgical gauze wrapped on the stem of Q-tips[®], portioned and then frozen before trials. Commercial samples 1 and 2 were kept in their original bottles and refrigerated at $\sim 2^{\circ}\text{C}$ between trials. Saturation was performed by transferring a small amount of sample 1 or 2 in to a clean glass flask which was then absorbed by Q-tips[®] until saturated (0.2 ml). Sample 4 was purchased on trial days immediately prior to testing. Saturation protocol for 4 was the same as for samples 1 and 2. Sample 3 was frozen at $\sim -18^{\circ}\text{C}$ immediately after collection. Portions of 3 were thawed prior to use, and data collection for this scent was completed within 72 h. During trials, samples of a scent were exchanged between trials if contact was made by subjects or after a maximum of 15 min if no contact was made. In addition, the replica or box was swabbed with isopropyl alcohol (99%) following any contact by subjects.

All data were collected between the hours of 8:00am and 12:00pm on clear days between May and August at off-leash dog parks in Victoria, B.C., Canada. During data collection, the dog model and black box were situated so that subjects were able to approach from all angles, and with unrestricted access. The position of the model and black box was rotated regularly, and the location of scent sampling trials changed on consecutive days.

A total of 334 approaches were video-taped and evaluated. Of this total, 142 recordings were excluded (human or other dog interference during the

close approach, repeat visits from the same or an indistinguishable dog for the same scent). One hundred and ninety two recordings were useable ($N = 40$ estrus vaginal secretion, $N = 35$ coyote urine, $N = 53$ estrous white tail deer urine, and $N = 18$ food samples; control box: $N = 10$ coyote urine, $N = 17$ estrous white tail deer urine, and $N = 19$ food samples). Of the 192 useable recordings, 73 included repeat sniffers who were observed sniffing a different scent sample. No dogs were analyzed sniffing the same scent more than once. One hundred and nineteen different dogs ($N = 119$) were distinguished during video analysis. Trials with the estrus dog scent on the control box were halted when regional wild fires lead to major reduction in air quality and thus are excluded from analyses. For the multiple trials, a single scent was presented each day which was then altered on consecutive trial days. Videos were examined frame by frame and scoring initiated when the nose of the approaching dog was sniffing within 3 cm of the scent sample and halted when sniffing stopped, and the head of the dog moved out of a 3 cm radius from the sample (see [Figure 1](#)). We recorded the first nostril (right/left) used to sniff each of the samples and the last nostril (right/left) used when the dog terminated the encounters. Nostril use was defined by proximity to the sample and proportional flaring of the nares during sniffing. The proportional time spent sniffing by each nostril was assessed by tallying for each approaching dog the total time (seconds) of sniffing with each nostril. Sniffing was determined by rhythmic motion of the head, flaring of the nares, and changes in the direction of the rhinarium compared to the position of the head. Direction and position of the eyes was noted, if possible, during searching by the subjects to ensure sample acknowledgement.

We tested repeatability of the video scoring. A naive observer without familiarity to the hypothesis was asked to score 70 videos for the first and last nostril used in the encounters. Of these, 34 videos were also assessed for the total number of frames viewed for each nostril. Videos involved equal numbers of each odorant but randomly chosen sequences within each odorant. There was a 91% overlap between the original scores and the naïve analysis for first and last nostril use and a 92% correlation for the number of frames which produce results consistent with the full analysis. We used the full data set in our analysis.

Data were analyzed using paired t-tests (two-tailed) and chi-squared tests including heterogeneity and homogeneity tests tested against a 1:1 ratio. All analyses were done using SPSS v.24 (IBM, USA).

Results

An initial usage of the right nostril occurred in 68% of the encounters for the estrus dog vaginal secretion ($N = 40$; $\chi^2_1 = 4.90$, $p < 0.05$), 66% for deer urine (N

= 53; $\chi^2_1 = 5.45$, $p < 0.025$) and 69% for coyote urine ($N = 35$; $\chi^2_1 = 6.43$, $P < 0.025$) but no bias (50%) for the food sample ($N = 19$; $\chi^2_1 = 0$, $p = 1.00$). As the heterogeneity χ^2 was not significant ($p > 0.8$), we combined the three conditions which yielded a highly significant right nostril preference ($\chi^2_1 = 15.13$, $p < .001$). Similar trends were observed within the control box condition, 76% right nostril use for deer urine ($\chi^2_1 = 4.76$, $P < 0.05$), 80% right nostril use for coyote urine ($\chi^2_1 = 3.6$, $P = 0.06$) and no bias (36%) for the food sample ($\chi^2_1 = 1.32$, $p = 0.25$) (Figure 2). The nostril used at the completion of each sniffing event also tended to be right-biased although the effects were weak in all cases ($P > 0.1$).

Among the four different scents that we used on the dog model, average sniff duration was highest for estrus dog ($\bar{x} = 2.46$ s, range = 0.40 s–6.03 s), lower for coyote and estrus deer ($\bar{x} = 1.18$ s, range = 0.23 s–5.10 s, and $\bar{x} = 1.19$, range = 0.27 s–3.90 s) and lowest for dog food ($\bar{x} = 0.90$, range = 0.27 s–2.3 s; $F_{3,142} = 17.1$, $p < 0.001$). The three different scents on the control box were similar to those of the model box for dog food and estrus deer ($\bar{x} = 1.11$ s, range = .33 s–2.30 s and $\bar{x} = 1.30$ s, range = 0.47 s–3.73 s) but

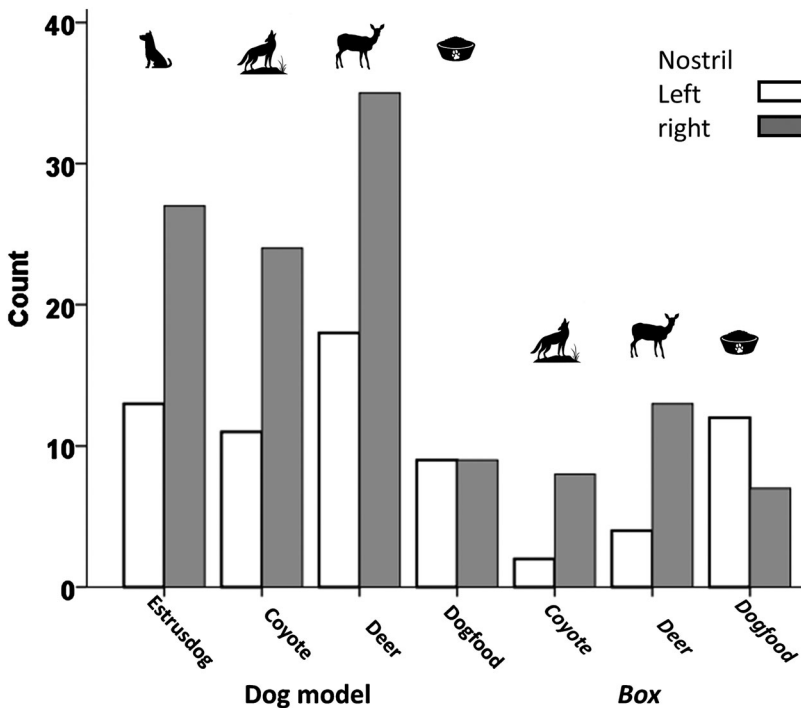


Figure 2. Left and right initial nostril use by off-leash dogs to experimental scents on a dog model and a box. Total number of approaches is 192. Experimental scents are vaginal secretions of an estrus dog, coyote urine, deer urine and wet dog food.

higher for coyotes ($\bar{x} = 2.49$ s, range = 1.07 s–4.70 s; $F_{2,43} = 10.3, p < 0.001$). The total time dogs spent investigating each scent with the left or right nostril was largely concordant with trends for initial nostril use. There was a marginally greater right nostril use (paired $t_{191} = 3.0, p < 0.004$; $F_{1,138} = 14.3, p < 0.001$), the effect being greatest for the estrus dog scent on the dog model (paired $t_{39} = 2.6, p < 0.06$) and the estrous deer scent on the control box (paired $t_{16} = 2.5, p < 0.03$) (Figure 3).

Discussion

Neurobehavioural studies of laterality stems from the *Approach-withdrawal Model*, which highlights the importance of the anterior cortical areas of the brain in emotional functioning, and suggests that the left hemisphere is more strongly involved in the processing of positive emotions related to an approach, whereas the right hemisphere is responsible for the processing of negative withdrawal-related emotions (Davidson, 1992; Schneider, Delfabbro, & Burns, 2013). In dogs, hemispheric dominance provides the proximal mechanism for tail wag laterality (Quaranta, Siniscalchi, & Vallortigara, 2007) as well as paw preference (Batt, Batt, Baguley, & McGreevy, 2009; Branson & Rogers, 2006; Plueckhahn, Schneider, & Delfabbro, 2016; Quaranta et al., 2006; Siniscalchi, Bertino, & Quaranta, 2014; Wells, Hepper, Milligan, &

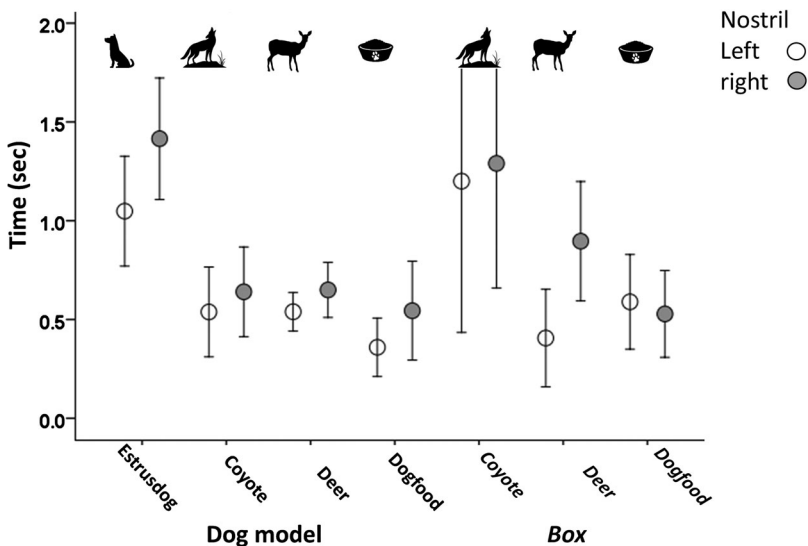


Figure 3. Length of time (sec) off-leash dogs used the left and right nostril for experimental scents on a dog model and a box. Total number of approaches is 192. Experimental scents are vaginal secretions of an estrus dog, coyote urine, deer urine and wet dog food.

Bernard, 2018), or head/eye orientation, (Barber, Randi, Muller, & Huber, 2016; Nagasawa, Kawai, Mogi, & Kikusui, 2013; Ratcliffe & Reby, 2014; Siniscalchi, Quaranta, & Rogers, 2008,) and possible signalling and communications (Artelle, Dumoulin, & Reimchen, 2010; Siniscalchi, Lusito, Vallortigara, & Quaranta, 2013).

Our data using unrestricted dogs and a model dog as an initial visual stimulus showed that in each experimental scent except for the scent of food, a pattern of right nostril bias was observed during novel olfactory investigations. These data agree with Siniscalchi et al. (2011), and are consistent with the perspective that the hypothalamic–pituitary–adrenal axis is mainly controlled by the right hemisphere, which indicate a higher state of arousal during the initial olfactory investigations (Craig, 2005).

There may be a fundamental difference in the way that canines process estrus vaginal secretion as compared with components of urine. Although both urine and vaginal secretion would elicit activity from the vomeronasal organ (Adams & Wiekamp, 1984), the coded information is likely differentially processed.

Average total time spent investigating particular experimental scents differed between the dog model and the control box. The scent from the estrus vaginal secretion from a dog elicited a much longer investigative time on the model compared with the other scents. The combination of the estrus scent and the visual signals of the dog replica may have facilitated this longer investigation time. Within the control box condition, the longest investigation times were observed for the scent of coyote urine. Coyotes do not occur on Vancouver Island, B.C and would have comprised a novel canid scent for most of the dogs.

Freezing behaviour has been described as anxious arousal in humans and canines, and is related to parasympathetic inhibition of the motor system in preparation for action (Roelofs, 2017; Rogerson, 1997). If right nostril use is a true representation of arousal state in canines, then it is possible that the immobile dog model influenced some of the approaching dogs, leading to an expected bias of the right nostril. However, this trend was not observed for all scent samples.

Consistent with previous research by Siniscalchi et al. (2011), there was no nostril bias for food when considering the initial nostril used to sniff the sample. In addition, the scent of food was investigated by subjects for a shorter time than other scents and shifted predictably to investigations by the tongue. This did not occur with the other scents and it is probable that the scent of food offered reduced valence as a novel stimuli and was recognized quickly.

We have described here a simple field protocol that may be used to assess functional olfactory behaviour of canines in the field. The olfactory bulb plays a sensory as well as a modulatory role in the forebrain, hypothalamus and

limbic system, while the right hemisphere is associated with sympathetic activation of the hypothalamic–pituitary–adrenal axis which is linked to control of aggression and fear (Cain, 1974; Craig, 2005; Siniscalchi et al., 2011). If our results are representative, it raises the prospects that wild canids could also exhibit asymmetric nostril use in behavioural interactions. Bears (Ursidae), the sister group of canids, use olfaction as a primary sensory modality and exhibit lateralized paw use Reimchen and Spoljaric (2011) and would also be predicted to show olfactory laterality although the behavioural geometry of bear interactions or foraging has yet not been documented.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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