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Sniffing with the right nostril: lateralization of response to odour stimuli by dogs

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Lateralization in dogs, *Canis familiaris*, has been reported for paw usage and response to visual and acoustic stimuli. Surprisingly, however, no investigation of possible lateralization for the most relevant sensory domain of dogs, namely olfaction, has been carried out. Here we investigated left and right nostril use in dogs freely sniffing different emotive stimuli in unrestrained conditions. When sniffing novel nonaversive stimuli (food, lemon, vaginal secretion and cotton swab odours), dogs showed initial preferential use of the right nostril and then a shift towards use of the left nostril with repeated stimulus presentation. When sniffing arousal stimuli such as adrenaline and veterinary sweat odorants, dogs showed a consistent right nostril bias all over the series of stimulus presentations. Results suggest initial involvement of the right hemisphere in processing of novel stimuli followed by the left hemisphere taking charge of control of routine behaviour. Sustained right nostril response to arousal stimuli appears to be consistent with the idea that the sympathetic hypothalamic–pituitary–adrenal axis is mainly under the control of the right hemisphere. The implications of these findings for animal welfare are discussed.

Brain lateralization, both structural and functional, has been observed in several nonhuman species (Bradshaw & Rogers 1993; Rogers & Andrew 2002; Vallortigara & Rogers 2005), including canine species (Wells 2003; Quaranta et al. 2004, 2007; Siniscalchi et al. 2008, 2010a; Guo et al. 2009).

Functional lateralization at the population level has been reported for auditory and visual sensory modalities. For instance, an advantage of the right ear in processing conspecific vocalizations and of the left ear in processing threatening stimuli has been observed (Siniscalchi et al. 2008); visual stimuli of high emotional valence have been shown to elicit preferential turning to the left side, probably as a result of selective activation of contralateral brain structures (Siniscalchi et al. 2010c). As of yet, however, no lateralization research has been conducted on a most crucial sensory domain for dogs, *Canis familiaris*: that is, olfaction.

Studies suggest the presence of a lateralized process in the analysis of odours in both vertebrate and invertebrate species (Rogers & Andrew 2002; Royet & Plailly 2004; McGreevy & Rogers 2005; De Boyer Des Roches et al. 2008; Rogers & Vallortigara 2008). Domestic chicks, *Gallus gallus*, for example, show better discrimination of imprinting olfactory stimuli when using their right nostril (Vallortigara & Andrew 1994; Rogers et al. 1998) and stronger head shaking to a noxious odour under right nostril stimulation (Burne & Rogers 2002). Homing pigeons, *Columba livia*, show impaired initial orientation when olfactory input is confined to the right nostril only (Gagliardo et al. 2007). Horses, *Equus caballus*, show a population bias to use the right nostril first in response to stallion faeces (McGreevy & Rogers 2005) and in response to novel objects (De Boyer Des Roches et al. 2008). Honeybees show behavioural, electrophysiological and morphological asymmetries during olfactory learning favouring their right antenna during initial memory recall (Anfora et al. 2010; Frasnelli et al. 2010a,b).

In humans, despite findings demonstrating that basic olfactory perceptual processes appear lateralized between the hemispheres (summarized in Brancucci et al. 2009), some controversy exists over the hemispheric role in the processing of odours: although Broman et al. (2001) reported a right-nostril advantage for perceived odour familiarity, human neonates respond to an emotional positive odour (smells with a high affective valence and presumably with a high degree of familiarity) presented to the left

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nostril (left hemisphere) by head turning but do so significantly less often when the odour is presented to the right nostril (Olko & Turkewitz 2001). Furthermore in humans, a right-nostril dominance was also reported in unfamiliar but not familiar odour discrimination performance (Savic & Berglund 2000).

The aim of the present study was to investigate whether dogs show nostril asymmetries in processing odorants that differ in terms of familiarity and emotional valence during free sniffing behaviour under unrestrained conditions.

METHODS

Subjects and Housing

The subjects were 30 neutered mongrel dogs (15 males and 15 females) kept in a large rural kennel associated with the Faculty of Veterinary Medicine of Bari University, Italy.

All dogs, aged between 2 and 8 years (5.4 ± 1.04; mean years $\pm$ SE), were housed individually in a large area (270 m^2) with 30 runs separated by cement block partition walls (2.50 m high), concrete floors and an exposed rafter ceiling (2.50 m high). Each run comprised two sections: an indoor insulated section (sleeping area, 3 m^2) and an outdoor section (6 m^2) joined by a gangway that could be closed by a metal door. Dogs were confined to the sleeping area overnight (1900–0700 hours) to prevent extremes of temperature (temperatures range between an average minimum of 17 °C in winter and an average maximum of 25 °C in summer). Suitable bedding equipment was also provided and was periodically cleaned and sanitized. During the day, the environment was illuminated with a combination of natural and fluorescent light. Complete commercial food for adult dogs was provided twice during the day at approximately 0700 and 1800 hours, whereas water was available ad libitum.

Clinical examination and coprological analyses for parasites were carried out for all the dogs in the sample. In addition, dogs were conducted daily for a walk (about 40 min per day) into an exercise area inside the kennel.

The experiment was carried out in a large room (4×5 m and 3 m high) isolated from the rest of the kennel, where each dog was kept on a lead separately during the test.

Testing Apparatus and Procedure

The study involved presentation of dogs with different olfactory stimuli to assess whether there was any tendency to use one nostril preferentially rather than another during sniffing behaviour.

Odorants used as test stimuli were presented on cotton swabs commonly used for canine vaginal cytology (FL Medical, Torreglia, Italy). Odorants used comprised: (1) food (complete commercial food for adult dogs; Royal Canin, Milan, Italia); (2) sweat of the veterinarian associated with the kennel; (3) lemon; (4) adrenaline (Adrenaline F.U. 1 mg/1 ml Galenica Senese, Siena, Italy); (5) oestrous bitch vaginal secretions; and (6) the cotton swab without any particular odour. Odorants were changed regularly to keep the odour quality constant.

The veterinarian was instructed not to use deodorant/antiperspirant for 2 days before the experiment until after the collection of the swab was over, and to take only a shower on the morning of the experiment. On the day of the collection, the cotton swab was placed under the armpits of the vet for 10 min and then stored at −80 °C until testing (several samples were collected).

Lemon odour samples were obtained directly from natural lemon juice and then stored at −80 °C.

Oestrous secretion was sampled by inserting the cotton swab directly through the vulvar lips into the vagina of a healthy bitch who showed both clinical and behavioural signs of oestrous. Different samples were collected and then stored at −80 °C until the experiment.

The cotton swab impregnated with different odours was installed on a digital video camera located on a tripod in the centre of the testing area (see Fig. 1); the tripod and the entrance of the

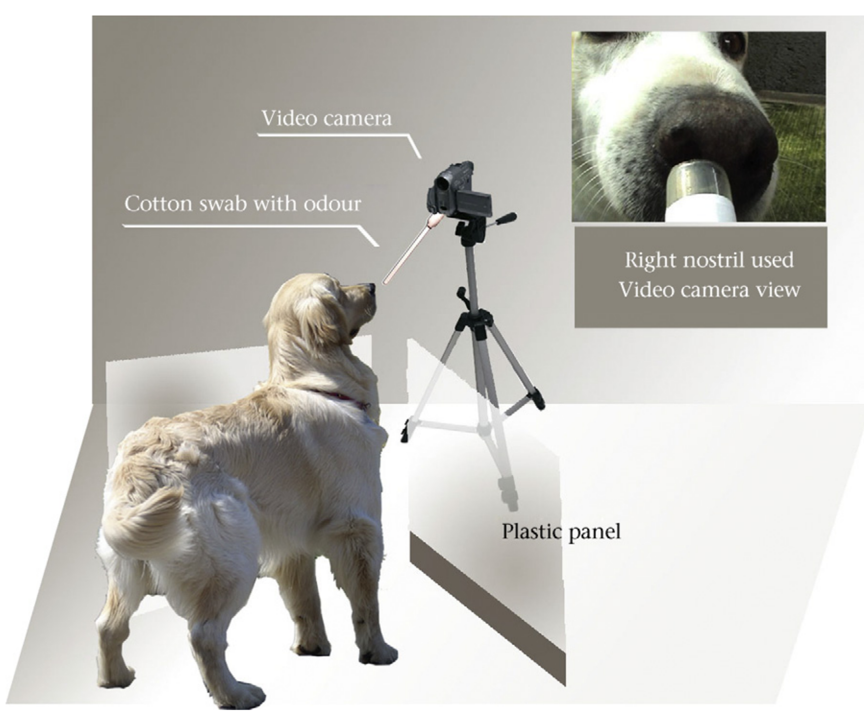

Figure 1. Schematic representation of the testing apparatus.