# Olfactory lateralization in non-human mammals: a mini-review

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## Abstract

The asymmetric use of nostrils and few contralateral projections in olfactory neural pathways allow us to suppose the dominance of one hemisphere in the processing of various odours in non-human mammals. Although olfaction is the most important sensory domain for many mammals, lateralization of this sense is poorly studied in this group of animals, and the existing limited knowledge is based on experiments on laboratory and domestic mammals. Here we review the most important studies in this developing field, with an emphasis on the methods used. Most of the recent studies indicate the dominance of the right hemisphere in the processing of social and aversive odours and analysis of familiarity of the olfactory stimuli. Dominance of the left hemisphere was found only in a form of a slight trend in the perception of food odour. Almost all existing results on olfactory lateralization are in line with the well-studied patterns of visual lateralization. However, further focused investigations are needed to confirm this consistency. Studies on a wider range of species and stimuli will help to get a better understanding of the relative hemispheric roles in olfactory perception.

**Keywords:** olfactory lateralization, nostril use, sensory lateralization, brain asymmetry, mammals

## Introduction

Sensory lateralization is often manifested as unequal use of paired sensory organs, which leads to the primary processing of stimuli by one of the hemispheres. Such biases occur primarily due to the specialization of the hemispheres towards specific functions and cognitive processes. The vast majority of current studies of sensory lateralization in non-human animals were focused on visual asymmetries (Vallortigara, Chiandetti and Sovrano, 2011; Rogers, Vallortigara and Andrew, 2013). Fewer studies provide information on olfactory lateralization, presumably due to the difficulties with estimating the use of one nostril, especially in the wild. Yet the anatomy of the olfactory system provides the possibility of estimating the use of one hemisphere. Most neural projections from each nostril do not cross, and the information goes to the ipsilateral hemisphere (Shipley and Ennis, 1996). In mammals, the perception of smell starts with the sensory olfactory neurons located in the nasal epithelium. Axons of these neurons project ipsilaterally to the olfactory bulb (OB), and axons of OB cells form the lateral olfactory tract which ipsilaterally projects to the primary olfactory cortex, which consists of the anterior olfactory nucleus, olfactory tubercle, the piriform cortex (PC), amygdala and the entorhinal cortex (de Castro, 2009).

The bulk of evidence supports the idea that the olfactory perceptual processes are lateralized in humans (Royet and Plailly, 2004; Brancucci et al., 2008) In general, mammals are the most extensively studied group in terms of olfactory lateralization, with only a few reports on other vertebrate taxa (Siniscalchi,

**Citation:** Berezina, E., Giljov, A., and Karenina, K. 2022. Olfactory lateralization in non-human mammals: a mini-review. Bio. Comm. 67(1): 49–56. https://doi.org/10.21638/spbu03.2022.105

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**Manuscript Editor:** Anton Nizhnikov, Department of Genetics and Biotechnology, Faculty of Biology, Saint Petersburg State University, Saint Petersburg, Russia

**Received:** August 31, 2021;

**Revised:** September 23, 2021;

**Accepted:** October 1, 2021.



**Funding:** This work was supported by the Russian Science Foundation (grant No. 19-14-00119).

**Ethics statement:** This paper does not contain any studies involving human participants or animals performed by any of the authors.

**Competing interests:** The authors have declared that no competing interests exist.

2017). Asymmetry of smell perception has been shown for some bird species, e.g., chicks (*Gallus gallus*) discriminated the smell of an imprinted object better with the right nostril (Vallortigara and Andrew, 1994) and showed more head-shaking responses to the adverse stimuli presented to the right nostril (Burne and Rogers, 2002). The importance of olfactory input from the right nostril, but not from the left, was shown in homing pigeons, who failed in navigation while using only the left nostril (Gagliardo et al., 2011). Several studies provided evidence of lateralization even in invertebrate species — honeybees (*Apis mellifera*) showed an increased ability to recall memories about an odour associated with sugar reward one hour after the presentation if it was presented to the right antenna (Anfora et al., 2010). Such asymmetry is also demonstrated within the morphological structure of antenna — the right antenna of the honeybee has more olfactory sensilla than the left antenna (Frasnelli et al., 2010). Population-level preference in antennal contacts was found in red wood ants, *Formica rufa*. The "receiver" ants used their right antenna significantly more often than the left one during food exchange through trophallaxis (Frasnelli et al., 2010).

Olfaction is an important sensory modality for many vertebrates, especially mammals, sometimes even more important than vision (Nielsen et al., 2015). Therefore, the evaluation of lateralization in the processing of olfactory signals by mammals can give us useful insights for sensory lateralization in this group of animals. Although a sufficient number of experimental studies have provided evidence for the existence of lateralization in mammalian olfaction, few papers generalized current findings and compared them with existing evidence of lateralization of other senses. Therefore, the purpose of this review is to summarize current knowledge about olfactory lateralization in non-human mammals and compare the patterns of olfactory lateralization with those of visual lateralization. The main methods used in these studies on mammals are also discussed.

## Variety of manifestations of olfactory lateralization in mammals

Rodents are the group of mammals who predominantly rely on olfaction in communication, predator avoidance and search for food (Knaden and Hansson, 2014). Several studies have focused on the lateralization of common laboratory rodents, rats (*Rattus norvegicus*). A positive correlation was found between behavioural responsiveness to a neutral odour and activation of the left olfactory cortex (Litaudon et al., 2017). Rats with ablation of the left olfactory bulb were impaired in their behavioural reaction to a negative odour (smell of a stressed conspecific), but not in a hormonal response (Dantzer, Tazi and Bluthé, 1990). Lateralization of olfactory memory formation is task-specific in rats — their left piriform cortex (PC) activates more during the initial stages of olfactory-cued learning, which was registered as an increase of membrane-associated protein kinase C in the left PC (Olds et al., 1994) and as an increase of oscillatory activity in the left anterior PC (Cohen, Putrio and Wilson, 2015). Asymmetry of PC activation is accompanied by right orbitofrontal cortex (OFC) bias during initial odour discrimination learning; right OFC also activates more than left during reversal learning (Cohen and Wilson, 2017). Overall, these findings partly contribute to the idea that the left hemisphere participates in emotional response to odours, while the right hemisphere activates more during memory formation and familiarity rating. These two processes are closely related, yet sometimes activation in different tasks is observed in another hemisphere too, which reveals the complexity of olfactory information processing (Royet and Plailly, 2004).

Another intriguing direction of research is asymmetries in nostril use during the perception of olfactory stimuli of different valence. Pioneering research in this field was conducted by McGreeevy and Rogers, who presented an olfactory stimulus to thoroughbred horses, *Equus caballus* (2005). The study, conducted on 157 horses, revealed a preference to use the right nostril while investigating stallion faeces for the first time among horses younger than four years old. Another experiment performed on 37 adult purebred Arab mares showed a slight bias to sniff objects with neutral or negative valence with the right nostril (67 % of mares; results didn't reach significance); the right nostril was used more often for investigation of a neutral novel object, than for investigation of a negative one (de Boyer Des Roches et al., 2008). In both studies, the authors propose that the preference registered reveals dominance of the right hemisphere in assessing novelty.

The preference to use the right nostril was also reported for 12 jumper horses smelling adrenaline and urine of oestrous mares (Siniscalchi et al., 2015). Higher cardiac activity of horses was recorded when sniffing adrenaline with the right nostril as compared with the left. This result supports the hypothesis of the dominance of the right hemisphere in stressful situations associated with the expression of intense emotions, mainly through the control of the hypothalamic-pituitary-adrenal axis (Rogers, Vallortigara and Andrew, 2013). Smelling of urine with the right nostril was associated with higher cardiac activity and more frequent flehmen, which reveals dominance of the right hemisphere in control of sexual behaviour.

Another possible piece of evidence for lateralization of perception of odours of a sexual context comes from research on wild Asian elephants (*Elephas maximus*). The study focused on motor asymmetries of trunk use and revealed a right-sided preference of male elephants

**Table 1. Summary of the studies of lateralized olfactory processing in mammals**

| Species | Study | Hemispheric dominance | Reference |
|---|---|---|---|
| Laboratory rat (*Rattus norvegicus)* | Greater activation of PC and amygdala correlated with behavioural responsiveness | Left | (Litaudon et al., 2017) |
| | Impairment of appropriate behavioural reaction to the smell of the stressed conspecific due to a lesion | Left | (Dantzer, Tazi and Bluthé, 1990) |
| | Higher activation of PC during initial stages of olfactory-cued learning | Left | (Cohen, Putrio and Wilson, 2015; Olds et al., 1994) |
| | Higher activation of OFC during initial stages of olfactory-cued learning and reversal learning | Right | (Cohen and Wilson, 2017) |
| Laboratory mouse (*Mus musculus*) | Sniffing female urine and vanilla | Right | (Jozet-Alves, Percelay and Bouet, 2019) |
| | Sniffing aversive odour (rat odour) | Left | |
| Horse (*Equus ferus caballus*) | Sniffing novel odour (stallion faeces) | Right | (McGreevy and Rogers, 2005) |
| | Sniffing neutral novel object and negatively conditioned object | Right | (de Boyer Des Roches et al., 2008) |
| | Sniffing adrenaline and urine of oestrous mares | Right | (Siniscalchi et al., 2015) |
| Dog (*Canis lupus familiaris*) | Sniffing novel nonaversive stimuli (food, lemon, vaginal secretion, cotton swab)<br>Sniffing aversive stimuli (adrenaline and veterinarian odour) | Right | (Siniscalchi et al., 2011) |
| | Sniffing an odour of stressed conspecific | Right | (Siniscalchi, d'Ingeo and Quaranta, 2016) |
| | Sniffing an odour of stressed human | Left | |
| | Sniffing an odour of oestrous vaginal secretion, coyote and deer urine | Right | (Brown and Reimchen, 2019) |

Note: PC — piriform cortex, OFC — orbitofrontal cortex

in trunk-to-genitals movements (Giljov, de Silva and Karenina, 2017). As the authors propose, lateralization of truck movement might reflect a preference to use the right nostril, which, in turn, reflects the dominance of the right hemisphere in processing social information.

Dogs, *Canis familiaris,* were also studied for olfactory stimuli perception. In the set of experiments performed by Siniscalchi et al. (2011), 30 dogs were presented with different emotive stimuli. Dogs in unrestrained conditions preferred to use their right nostril to sniff novel nonaversive stimuli (food, lemon, bitch vaginal secretion and cotton swab odours) during the first presentations of these stimuli. However, during subsequent presentations, preference shifted towards the use of the left nostril. These results follow the common pattern of lateralized perception of novelty: initially, novelty is assessed by the right hemisphere and then dominance shifts to the left hemisphere, which controls routine responses to stimuli which have become familiar. Two aversive stimuli — adrenaline and veterinarian odour — were sniffed with the right nostril consistently during all presentations. Registered dominance of the right hemisphere might be associated with the fact that both these stimuli are clearly aversive, thus producing intense emotions which are controlled by the right hemisphere through dominance in sympathetic system activation (Craig, 2005). Dogs moving freely at off-leash dog parks showed similar right nostril bias when sniffing the odour of oestrous dog secretions, deer urine and coyote urine (Brown and Reimchen, 2019).

In a more recent study, right nostril preference was also found in dogs sniffing an odour of a stressed conspecific (after 5-minute isolation) (Siniscalchi, d'Ingeo and Quaranta, 2016). The authors assumed that the perception of stress signals from a conspecific enhances the arousal state of the dog (reflected in higher cardiac activity), thus leading to the activation of the right hemisphere. When sniffing the odour of humans in the state of arousal (fear, running), left nostril bias was found in dogs. In this case, the shift to the left hemisphere may be explained by the greater involvement of the left amygdala, which plays a greater role than the right amygdala in accurate determination of threat (Morris et al., 1996; Hardee, Thompson and Puce, 2008). More precise processing of the aroused human odour may be needed since a threat to the human is not necessarily a threat to the dog. Another possible explanation is based on the idea that the left hemisphere is responsible for approach motivation, and the dog may experience the urge to pursue a stressed human as possible prey.

Preference for nostril use in unrestrained conditions was also tested in 40 male laboratory mice (*Mus musculus*) (Jozet-Alves, Percelay and Bouet, 2019). Mice used their right nostril to sniff the odour of female urine and vanilla and the left nostril to sniff aversive stimuli (rat odour eliciting anxiety responses in mice (Anisman et al., 2001)). Although the preference to use the right nostril to sniff social odours is consistent with the literature on other species (e.g., McGreevy and Rogers, 2005; Siniscalchi et al., 2015), the use of the left nostril to sniff aversive stimuli is contrary to the common idea of the involvement of the right hemisphere in processing negative emotions. What is more, the preference to use the right nostril to sniff positive odours (female urine and vanilla) and the left nostril to sniff negative odours (rat) is in opposition with the widely accepted valance hypothesis, proposing that the left hemisphere is dominant in processing positive emotions, and the right hemisphere — in processing negative emotions (reviewed in Najt, Bayer and Hausmann, 2013). Further studies might be helpful to determine whether this pattern is specific only to laboratory mice or is more common among mammals.

Summarizing all of the above, although there are species showing contrary results, most of the research reveals similar patterns — dominance of the right hemisphere in accessing novelty of the odour, and in the processing of social and aversive odours (summarized in Table 1). More research is needed in this field to make any conclusions about the division of roles of the hemispheres in olfaction. More species of different groups of mammals should be tested, especially those that particularly rely on the sense of smell. The use of more variable stimuli may also be important, especially those that may reveal a left-hemispheric dominance, according to the previous studies.

## Behavioural methods of studying olfactory lateralization

Behavioural methods of assessing olfactory lateralization are rapidly developing. Throughout the last 10 years, there has been a visible growth in the number of studies using a behavioural approach towards examination of the lateralized perception of odours, possibly because of their ease of implementation and reduced impact on experimental animals. Testing of olfactory biases is a particularly useful tool for investigations of lateralization in animals with eyes placed binocularly (e.g., in carnivorans), as evaluating their visual lateralization is complicated.

The odours presented to the tested animals vary depending on the purpose of the experiment. It may be food odours (vanilla odour for mice, commercial canine food), social odours (female vaginal secretions, faeces (Fig. 1, A), gland secretions), adrenaline or other stressful or aversive stimuli, like the sweat of a familiar veterinarian (McGreevy and Rogers, 2005; Siniscalchi et al., 2011, 2016; Jozet-Alves, Percelay and Bouet, 2019). Sometimes, the stimulus used in the experiment has no particular odour, so it is usually described just as "novel" for an animal. Special attention is usually paid to the familiarity and emotional valence of the presented stimuli, as these characteristics influence the manifestations of lateralization.

Experimenters using different kinds of odorants usually use a standard cotton swab to present an odour, which helps to avoid the influence of the visual form of the smelly substance (Siniscalchi et al., 2011, 2015; Brown and Reimchen, 2019) (Fig. 1, B). There are different ways of presenting an odour to an animal: it can be placed on the ground of the testing space (or above the ground at the level of the nose of the tested animal), which allows the animal to examine it freely (de Boyer Des Roches et al., 2008). Another method is presentation from the hands of an experimenter (McGreevy and Rogers, 2005). Presentation of stimulus to smaller mammals, like rodents, is more complicated — it requires a special testing apparatus, where the smell can be delivered through a pipette (Jozet-Alves, Percelay and Bouet, 2019). The measurements made during the experiment usually include recording of the first and the last nostril used, the total number of sniffs during the experiment and the time spent sniffing an odour. Tested animals can be equipped with devices that measure their physiological state, for example, a cardiac monitoring device (Siniscalchi et al., 2015), which allows measurement of the state of alertness of an animal in response to an odour.

In experiments with the animals moving freely, it is crucial to attract the animal to the source of the smell. For these purposes, a conspicuous visual stimulus can be used. For example, to attract dogs moving freely in an off-leash park to smell an object, experimenters built a full-size dog replica and placed an odorant source and camera between its hindlegs. During a set of experiments on saiga antelope (*Saiga tatarica)* novel objects of different shapes were placed near the waterhole in the natural setting of the nature reserve. The mobility of their prolonged nose (forming a small proboscis) allowed authors to measure asymmetrical nostril use — it curved to the side of the nostril used to sniff the object during approach (Fig. 1, C) (Berezina, Gilev and Karenina, 2021).

## Consistency between olfactory and visual lateralization

Visual lateralization is arguably the most studied sensory lateralization in both animals and humans (Güntürkün, Ströckens and Ocklenburg, 2020). In contrast to olfac-

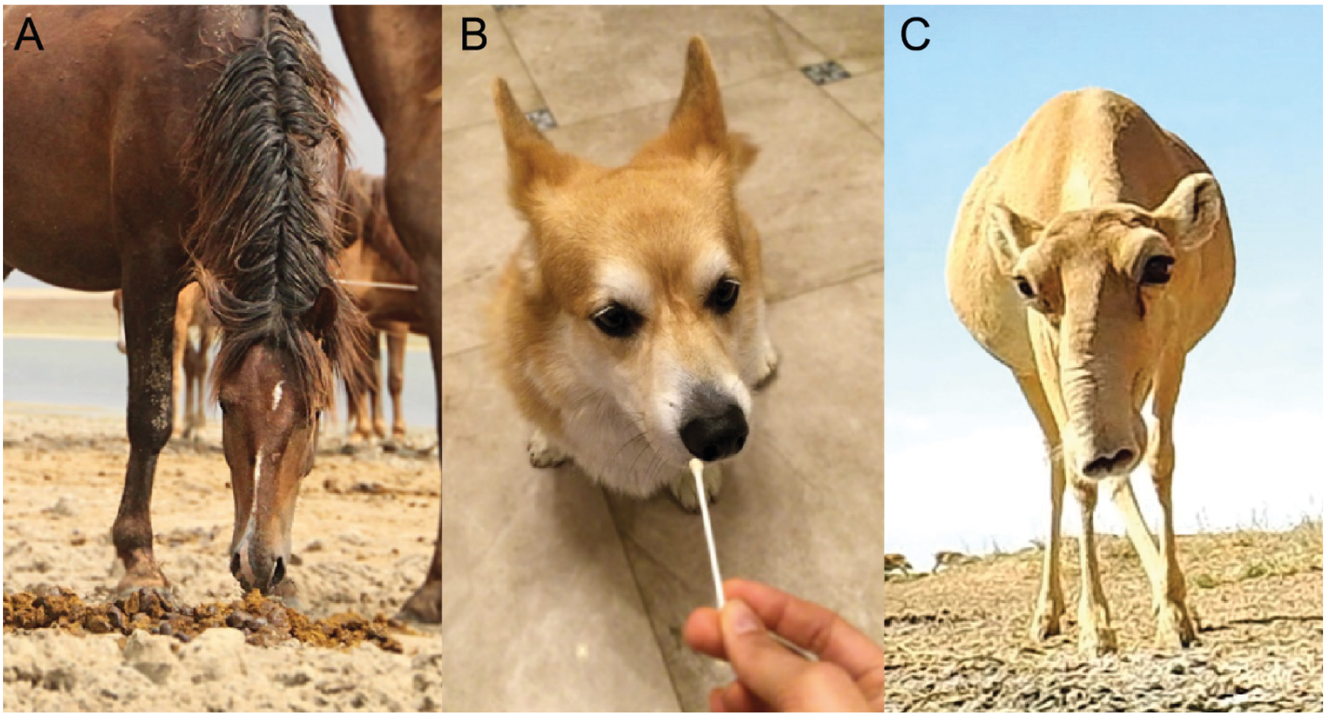


**Fig. 1.** Methods of olfactory lateralization assessment. (A) In horses, lateralized nostril use was recorded during sniffing of conspecific faeces. (B) In the experiment, dogs were presented with odour stimuli using a cotton swab. (C) Asymmetric nostril movement during sniffing which is typical for saiga antelopes allowed investigation of olfactory lateralization in this species in the wild.

tory projections, visual projections cross, i.e., the dominance of one hemisphere will cause contralateral eye preference and ipsilateral nostril preference. Overall, existing data on olfactory lateralization corresponds to the generalized model of the division of roles between hemispheres, based on the extensive amount of literature on visual lateralization (Rogers, Vallortigara and Andrew, 2013).

A reaction to novelty is the most investigated behaviour in terms of olfactory lateralization. Results of different studies consistently indicate right nostril preferences for novel odours, implicating right hemisphere dominance. This is in line with the reports of visual preferences: animals tend to use the left eye to observe novel objects (Rogers and Anson, 1979; Larose et al., 2006; Robins and Rogers, 2006). The dominance of the right hemisphere in reactions to novelty is consistent with the idea that the right hemisphere controls the hypothalamic-pituitary-adrenal axis, associated with the control and expression of intense emotions (Rogers and Andrew, 2002). This may explain the preference to use the right nostril to sniff arousing smells (adrenaline and the odour of a veterinarian) and the corresponding preference to use the left eye during vigilance (Martín et al., 2010; Austin and Rogers, 2012; Bonati et al., 2013), or while observing a predator (Hook-Costigan and Rogers, 1998; Braccini et al., 2012). Controversial results were obtained in experiments on mice, which showed a preference to use the left nostril to sniff aversive rat odour. Authors hypothesized that this result can be explained by the differential contribution of the right and left hemispheres to the stress response. The right hemisphere is responsible for long-term response to a stressor (Carlson et al., 1991), while the left hemisphere is involved in the initial stages of the stress response (shown for other olfactory tasks (Cohen, Putrino and Wilson, 2015; Cohen and Wilson, 2017)).

Another function of the right hemisphere is control of sexual behaviour, which is manifested as a right nostril preference in males when sniffing an odour of females in dogs and mice. In line with this, the bias to use the left eye was found in copulatory behaviour (Rogers, Zappia and Bullock, 1985). The large amount of evidence showing the left eye-right hemisphere advantage in social interactions in general (reviewed in Karenina et al., 2017) confirms the consistency between visual and olfactory lateralizations.

The studies of olfactory lateralization in feeding behaviour are scarce. However, a slight tendency to use the left nostril to sniff food objects corresponds to the results of studies of visual lateralization. Preference to use the right eye to look at food objects was found in various species (Kruper, Boyle and Patton, 1966; Rogers, Ward and Stanford, 1994; Vallortigara et al., 1998).

To summarize, the current limited knowledge indicates the general consistency between olfactory and visual lateral biases in mammals. However, the comparability of results on different modalities is limited since they were mostly obtained in different studies. Most behavioural experiments to test olfactory lateralization include the presentation of an odour centrally in front of the animal. In response to such presentation, the animal slightly turns its head to sniff the stimulus with one nostril, which, in turn, leads to a small bias in the visual field used. Nevertheless, studies testing both visual and olfactory lateralization simultaneously and assessing the link between them are lacking. Interesting evidence comes from the study performed on cows (*Bos taurus*), where they were presented with novel objects placed bilaterally. Cows showed a bias to right-sided head turn during visual inspection (right visual bias) but preferred to touch the object on the left side with their nose (Kappel et al., 2017). The authors doubt that head turns to the left indicate lateralized olfactory perception because cows touched it with the centre of their nose (no asymmetric nostril use was registered). However, the initial turn of the head to the left might reflect cows' attention to the novel odour initially sniffed with the left nostril. The touching of the object at later stages of object investigation served for getting more information. Thus, the left-side bias in head turns possibly indicates the greater reactivity to olfactory stimulus located on the left side. If this is the case, this study provides a striking example of the consistency between visual and olfactory lateralization, as both results imply the dominance of the left-brain hemisphere.

## Conclusion

There is no doubt that further research is necessary to broaden our understanding of asymmetry in the olfactory system. It is important to investigate a wider range of species, especially beyond domesticated and laboratory animals. This will help us to gain knowledge about the role of olfactory lateralization in an animal's routine behaviour in natural settings.

The use of more diverse stimuli will allow us to get a more complete picture of hemispheric roles in the processing of olfactory information. For example, very little is known about lateralization in the olfactory perception of food objects, orientation cues and group members.

The influence of an individual's level of curiosity on the manifestations of olfactory lateralization has not yet been measured. As it influences manifestations of visual and auditory lateralization (Hausberger et al., 2021), it might be important also to measure the degree of sensory exploration during the presentation of olfactory stimuli. A higher level of lateralization might be expected for less curious animals, i.e., showing more focused attention to the stimuli and less movement.

The investigation of olfactory lateralization along with visual lateralization in the same individuals and in response to the same types of stimuli is a promising direction of research, which may help to get a better understanding of the interrelations between lateralization of different sensory modalities. This may be particularly important for studies on mammals since, in these animals, olfaction and vision are the most significant senses.

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