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The effect of sex and age on paw use within a large sample of dogs (*Canis familiaris*)

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ABSTRACT

Many studies have focused on handedness as proxy for lateralization, highlighting that population-level biases in handedness seem to be characteristic of most animals, although the strength and direction varies between species. Gender has been found to influence handedness in some species; in humans, for instance, males are more likely to be left-handed than females. Another aspect that has been comparatively unexplored is the role of age in shaping functional asymmetries, especially in adulthood.

Handedness has been widely explored in dogs (*Canis familiaris*), although there are contrasting findings about the influence of the dogs' sex and age, possibly due to the comparatively small sample sizes used in previous studies. Here we overcame this issue by investigating these effects in a unique sample of 17,901 dogs of unknown neutered status. Specifically, this study used pre-collected data from the British Broadcasting Corporation (BBC)'s 'Test Your Pet' survey, during which owners tested their dogs' paw preference in retrieving food from a tube in 3 consecutive trials. Based on the results of these 3 trials, owners were asked to assess whether their dogs used their left or right forepaw most of the time, or if it was difficult to tell. 13,240 dogs were scored as having a paw preference (i.e., were not ambidextrous or ambiguous), representing 74.0 % of the dogs tested. In those dogs that showed a paw preference, there was a population-level right-paw preference in both male and female dogs (60.7 % female and 56.1 % male), however, the proportion of dogs with a right-paw preference was significantly higher in females than males. Elderly dogs also tended to show a stronger right-paw preference than younger dogs. We conclude that the effect of sex on handedness may be influenced by factors such as sex hormones, while age changes may reflect the development of handedness and its maintenance in dog populations.

1. Introduction

Lateralization suggests that the brain's hemispheres are functionally specialised in an asymmetrical manner, as revealed by behavioural asymmetries in sensory and motor functions (Ocklenburg and Güntürkün, 2017). Lateralization occurs in most animals, including vertebrates and invertebrates (Frasnelli, 2013; Rogers et al., 2013). Appendage laterality, or handedness/paw preference, is the most common way of measuring motor laterality in humans and non-human animals (Versace and Vallortigara, 2015). Handedness is assessed by observing the use of an animal's appendage when engaging in various activities (Batt et al., 2007). About 90 % of the human population is predominately right-handed, and this is consistent across all cultures and whilst in utero (Papadatou-Pastou et al., 2020). Lateralization is thought to be beneficial to individuals as it improves the efficiency of behaviours (Rogers et al., 2013). For example, chimpanzees with a stronger hand preference have been found to forage for termites more efficiently (McGrew and Marchant, 1999) and locusts with a stronger leg preference, make fewer mistakes while crossing a gap, suggesting improved motor control (Bell and Niven, 2016).

Lateralized behaviours have been reported in dogs (*Canis familiaris*) in a variety of tasks (reviewed in Siniscalchi et al., 2017; and Wells, 2020) and may be linked to increased motor and cognitive abilities (Tomkins et al., 2012). For example, left paw departure laterality is suggested to be associated with increased performance in dogs when performing tasks that involve forward movement such as following their handler, and searching and fetching objects (Van Alphen et al., 2005). Dogs exhibit lateralization in vision (Siniscalchi et al., 2010), olfaction (Siniscalchi et al., 2011, 2016a), and hearing (Andics et al., 2014, 2016; Ratcliffe and Reby, 2014; Reinholz-Trojan et al., 2012; Siniscalchi et al., 2008). Several studies have focused on cerebral lateralization with regard to emotional processing in dogs, providing evidence that the left

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and right hemispheres control the positive and negative emotions respectively (for a review see Siniscalchi et al., 2017). For example, the direction of a dog's tail wagging indicates an emotional response: the tail wags with higher amplitude towards the right when the dog is approached by a known individual, whereas it wags with higher amplitude towards the left when an unfamiliar dog or a cat approaches (Quaranta et al., 2007). Noise phobias have also been linked with lateralization: when presented with negative auditory stimuli (e.g. barking or thunderstorms), dogs use their left ear significantly more than their right ear (Siniscalchi et al., 2008). Moreover, dogs with non-significant pawedness were found to be more reactive to negative auditory stimuli that dogs with significant pawedness, suggesting a link between noise phobias and absence of overt handedness (Branson and Rogers, 2006).

It had been initially suggested that dogs, like humans, display a population-level bias to preferentially use the right forelimb, as shown, for example, when tasked with removing a plaster from over their eyes (Tan, 1987). However, unlike in humans, where there is a higher percentage of left handers in males than females (Hirnstein et al., 2019), studies involving dogs have reported that both males and females display predominant right-handedness in forelimbs (Branson and Rogers, 2006; Marshall-Pescini et al., 2013; Poyser et al., 2006; Schneider et al., 2013; Van Alphen et al., 2005), although other research has contested this or provided conflicting findings. For example, female dogs showed a significant preference for employing their right paw in paw lifting, whilst males preferred to use their left paw (Wells, 2003). Additionally, males show left paw preference and females show right paw preference when removing tape from their nose (Quaranta et al., 2004) and when using a Kong® feeding device (McGreevy et al., 2010). These sex differences have been observed in some, but not all studies; for example, in a recent meta-analysis Ocklenburg et al. (2019) found no overarching sex difference in dogs. This lack of agreement in the literature regarding the role of sex in handedness could be a result of several limitations, including methodologies (e.g. the assessment of neutered versus entire dogs), and inadequate statistical power.

Compared to our understanding of sex differences in laterality, comparatively little research has been conducted on the ontogeny of handedness, especially during adulthood. In humans, handedness is established between 4 and 6 years of age, and brains seem to become less lateralized with age (Agcaoglu et al., 2015). In primates, younger animals show less lateralization than adults (MacNeilage et al., 1987), however no such age-related effects have been reported in dogs (e.g. McGreevy et al., 2010; Schneider et al., 2013). Ageing in dogs can lead to deficits in cognition (e.g. learning, memory, and spatial awareness), as well as changes in patterns of sleep and how dogs interact socially (Landsberg et al., 2003). In cats, paw-preference seems to develop between 6 and 12 months and to remain stable thereafter (Wells and Millsopp, 2012). This may be related to hormones and sexual maturity, as at 12 weeks old cats do not show any paw preference (Wells and Millsopp, 2012); the same is true for kittens at 6–8 weeks old (Burgess and Villablanca, 1986). In humans, it has been suggested that mixed handedness (no preference of left or right) is strongly associated with atrophy of the hippocampus and amygdala due to age, but potentially also with other factors such as genetics, trauma in utero (i.e. bacterial infections, and alcohol exposure), and hormonal imbalances (Cherbuin et al., 2011). Alternatively, a loss of plasticity in dog behaviour (Milgram, 2003) could result in a more fixed lateralization in older dogs, as they may be less likely to alternate the paw they use compared to younger dogs with greater plasticity.

The aim of this study was to explore how sex and age influence dog pawedness. This was done by analysing the results of an extensive pre-collected dataset testing paw preference in dogs of different ages and sexes, containing data on the handedness of over 13,000 dogs from around the UK (BBC, 2004: Clarke et al., 2019).

2. Material and methods

2.1. Experimental design

Data were collected as part of the British Broadcasting Corporation (BBC)'s 'Test Your Pet' survey, in which a cross-sectional within-subject design was employed to collect information on dog and owner demographics, and performance in problem solving tasks, including a paw preference task (BBC, 2004; Clarke et al., 2019). The study consisted of three forms of data collection: (1) a survey concerning the pet-owner relationship and demographic information, but which did not ask about the neuter status of the dog; (2) tests carried out by the owner, including a food retrieval task designed to assess handedness or paw preference; and (3) a survey of the pets response to the television broadcast. Only section 1 and the paw preference task from section 2 were used for this analysis. This study was distributed to members of the public via the BBC website, the Radio Times magazine, and by phone call or text message.

For the food retrieval task, owners were asked to use a plastic or cardboard tube wide enough for their dog to reach into with its paw, and to place a treat near the end of the tube for the dog to reach. This was done three times in total. If the dog was not performing the behaviour, owners were asked to place the treat under a sofa and let their dog reach for it. Owners were then asked to score the test via three options: (a) the dog uses their left forepaw most of the time; (b) the dog uses their right forepaw most of the time; or (c) it is difficult to tell. A number of responses to the survey stated that the tested dog had a handedness of 'both' (4,661 out of 17,901 initial responses), and these were excluded from the dataset. As the BBC (2004) data was pre-collected, there was no control over what questions were asked of the owners. For instance, owners assessed their dogs' paw preference in 3 consecutive trials, but they only reported whether the dogs used the left or the right paw most of the times, or if it was difficult to tell. Had the owners provided information on the results of each trial of the Tube test they performed, this would have allowed for the calculation of a Handedness Index (Wells, 2003) for each dog, as is typically done in studies of this nature. However, it should be noted that while this test is comparatively crude, we consider it very unlikely that the nature of the task or the design of the study could have led to systematic biases in handedness with respect to age and sex (i.e. we can see no reason why owners would erroneously assign, for instance, right paw preference more frequently to females than males). However, we note that a study conducted in dogs by Wells (2003), reporting paw preferences in opposite directions for females and males, received considerable media attention, particularly in the UK. Therefore, we cannot completely exclude the possibility that this may have influenced owners' perception and shaped their responses.

The dataset we analysed contained information on 13,240 individual dogs (6,937 males, and 6,303 females), each of which was categorised into one of four age classes (Puppy [referred to as 'Baby' in the survey], Young Adult, Adult, and Elderly, based on the options available in the survey; Table 1). As dogs show a wide range of phenotype and longevity, defining age groups can be challenging, with timescales derived from a number of factors such as adult weight, behavioural changes such as playfulness or cognitive function and risks of age-related illness (Szabó et al., 2016; Epstein et al., 2005). As a consequence, a range of ages are used in defining when puppies become adult dogs, and when adult dogs

Table 1
Demographic information for the dogs included in the analysis (N = 13,240).

	Male (n = 6,937)	Female (n = 6,303)
Age		
Puppy	n = 677	n = 630
Young Adult	n = 3,142	n = 2,768
Adult	n = 2,558	n = 2,308
Elderly	n = 560	n = 597

are defined as senior or elderly dogs, with breed/size of dog most commonly cited as a defining factor. For example, primarily based on the achievement of adult weight smaller dogs are described as puppies up to about 9 months of age, whereas medium sized or larger dogs may not be considered adults until 12–18 months of age. In contrast due to the higher prevalence of age related illnesses in larger dogs, apparent signs of senility, and their reduced longevity compared to smaller or medium sized, larger dogs are considered senior from about 7 years of age, whereas the description tends not to be applied to medium sized or small breeds until 10–12 years of age.

2.2. Ethical note

The study was granted a favourable ethical decision by the Ethics Committee, School of Life Sciences, University of Lincoln.

2.3. Analysis

All analyses were conducted in R 3.6.3 (R Core Development Team). To test the effects of dog age class and sex on handedness, we fitted a generalised linear mixed-effects model using the glmer function in the lme4 package (Bates et al., 2015). Handedness was included as a binary response variable (with a logit link), with age class and sex (and their interaction) as fixed factors, and the unique id of the owner as a random effect to control for potential pseudoreplication caused by a single owner testing multiple dogs. Significance was determined by comparing the full model to a reduced model lacking the term of interest using a likelihood ratio test (Crawley, 2005). We also tested for differences over successive levels of the age class factor using planned difference contrasts (Puppy vs. Adult, and Adult vs. Elderly). Due to the lack of specific information on age classification in the survey we combined young adults and adults into one category named 'Adult'.

3. Results

Overall, out of the 17,901 initial responses, 13,240 dogs were scored to have a paw preference (i.e., were not classed as ambidextrous or ambiguous). Of these 13,240 dogs, 7,713 (58.3 %) showed a right-paw preference bias, which is significantly different from parity (binomial test: $p < 0.001$). This was the case for both male and female dogs (60.7 % female and 56.1 % male). Pawedness was significantly predicted to be influenced by the interaction between sex and age class ($\chi^2_2 = 8.43$, $p = 0.015$), as well as the main effects of both sex ($\chi^2_1 = 28.01$, $p < 0.001$) and age ($\chi^2_2 = 9.52$, $p = 0.009$), such that females had a significantly greater right-paw bias than males, and the proportion of right-paw preference was higher in older dogs (Fig. 1). Specifically, while there was no difference in pawedness between age classes for females ($\chi^2_2 = 2.78$, $p = 0.250$), males showed a significant difference overall ($\chi^2_2 = 15.19$, $p < 0.001$) with Elderly dogs exhibiting a significantly greater right-paw bias than Adult dogs (difference contrasts, Elderly vs. Adult: $z = -3.84$, $p = 0.002$; Adult vs. Puppy: $z = 0.56$, $p = 0.570$).

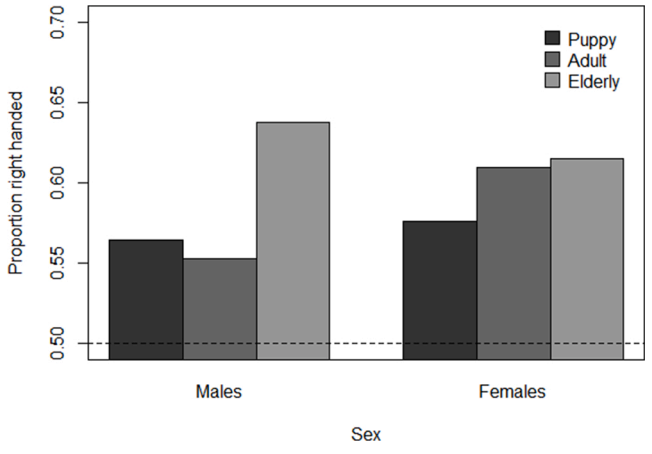

Fig. 1. Proportion of dogs with a right-paw bias as a function of sex and age class. The dashed horizontal line indicates an equal proportion of dogs with left- and right-paw biases.

4. Discussion

The main aim of this study was to identify the factors linked to paw preference in dogs, by analysing a large dataset of pre-collected data (BBC, 2004). Both males and females displayed right-pawedness in the food retrieval task with elderly dogs having significantly greater difference in paw preference compared to younger dogs.

Our study is based on data entirely collected by the dogs' owners and thus, lacks the scientific rigour of studies carried out in laboratories. In particular, there are three aspects to consider: i) the number of scores per individual dog; ii) the use of only one task; and iii) the influence of the media on the collection of the data. Regarding the first point, in the BBC study only three observation trials were carried out to provide a general score (i.e., left preference, right preference, or no preference) instead of a count of the individual paws used. With respect to this aspect, our study is methodologically different from the paw preference counts used in other work (e.g., in cats, McDowell et al., 2018; summarised in Wells, 2020). However, we see no reason to believe that the owners provided incorrect information, or that this could have led to a bias in a specific direction (e.g., toward the right paw). Moreover, we consider it very unlikely that any bias would be systemic across our large sample of more than 13,000 dogs.

In our study, owners were asked to test their dogs only in one task (the Tube test), a challenge where dogs have been previously shown to have a much weaker paw preference compared to tasks involving lifting a paw or removing an object (Wells, 2003). Testing dogs in several different tasks allow a better understanding of pawedness and a possible generalisation of the results. However, we also need to consider that different tasks may involve different motivations and/or emotional states of the tested animals, leading to results that are difficult to compare. For example, if a preference for the right paw when retrieving food suggests an involvement of the contra-lateral left hemisphere in tasks related to routine behaviours as foraging, a task where the dog is asked to remove a piece of tape from the nose may involve frustration, and may thus reveal an emotional hemispheric response over and above a mere motor bias.

Lastly, owners may have been influenced, in their data collection, by the media. In 2003 a study on sex differences in paw preference in dogs (Wells, 2003) was highlighted in the media, and may have resulted in inadvertent biases in owners' responses. Although we cannot verify, quantify or control for this, our analyses should be interpreted with this in mind.

Sex had a significant association with paw preference; it was found that female dogs displayed more right- than left-bias, which supports previous research (McGreevy et al., 2010; Wells, 2003). It was found that male dogs also displayed more right- than left-paw preference. Interestingly, females had a significantly greater right-paw bias than males, analogously to humans where there are more left-handed males then left-handed females (Hirnstein et al., 2019). This population level right-paw preference was supportive of Tan's (1987) early observations of tape removal by dogs, although others have disputed a population level paw preference or suggested differences in paw preference between sexes, citing sex-related hormonal effects (e.g. Wells, 2003). Right paw bias has also been recently reported in wolves (Regaiolli et al., 2020). Our study helps bridge the gap as it shows that although both female and male dogs in the sample scored to have a paw preference (i.e., those not classed as ambidextrous) are right-pawed overall, females are more right-pawed than males. This supports the hypothesis of a sex hormone influence on pawedness in dogs. Studies using a combination

of neutered and entire dogs typically do not find a sex difference (Batt et al., 2008; Schneider et al., 2013; Wells et al., 2017, 2019). The 'Test your Pet' survey did not ask owners to include the neuter status of the dogs (BBC, 2004), however, recent studies have suggested that around 57.1 % of dogs in the UK are neutered, including 55.0 % of males and 59.2 % of females (e.g. Sánchez-Vizcaíno et al., 2017), with 80 % of dog owners being open to neutering their dogs, and an additional 10 % doing so for medical reasons (Wongsaengchan and McKeegan, 2019). Therefore, it is likely that there is a mixture of neutered and entire dogs in such a large sample, with the majority being neutered. It is interesting to notice that, in UK, more females than males are neutered (Sánchez-Vizcaíno et al., 2017), and more females than males in our study were right-pawed. Thus, there may be a link between the neuter status and a preference to use the right paw, although we lack the data necessary to test this.

Age was significantly associated with pawedness, particularly in males, with Elderly dogs having a greater right bias in pawedness than Adult dogs. The concept that older animals would have more stable pawedness than younger animals was only previously conceptualised (MacNeilage et al., 1987), with more recent literature failing to find significance (McGreevy et al., 2010; Schneider et al., 2013; Wells et al., 2018). MacNeilage et al. (1987) suggest that this age-driven factor may be due to greater hand use inconsistencies in younger animals, specifically in monkeys. It is possible that as an animal ages, it learns which paw is more efficient to use, however the mechanism that governs this is not yet fully understood. Elderly dogs displayed a stronger paw preference, which conceptualises that the aforementioned dog cognitive decline (Landsberg et al., 2003) is not a factor in affecting pawedness as dogs age. Rather, it may support the theory that dogs lose behavioural plasticity as they age (Milgram, 2003). This could be investigated further by a longitudinal study that repeatedly measures stability of paw preference throughout the lifespan of a sample of dogs.

Research looking into pawedness preference in dogs is of importance, not only to increase understanding of the cognition of the species but also to improve their training, particularly for roles involving aiding humans (e.g. guide dogs, police dogs, and rescue dogs). If we have a better understanding of the strength of a dog's pawedness, it may increase their success during training for such roles and make it easier to determine which dogs are better suited for which roles. This has been extensively discussed in the review by Wells (2020) in this Special Issue, who cites a number of studies where paw preferences are associated with competency in other tasks as well as traits that may be desirable in dog training. For example, dogs which have a stronger pawedness, regardless of direction, are found to be more attentive during agility exercises compared to dogs with weaker pawedness (Siniscalchi et al., 2014), whilst Batt et al. (2008) and Tomkins et al. (2012) reported an association between pawedness and successful outcomes in guide dog training. Furthermore, left-pawed dogs display left visuospatial bias while right-pawed dogs display reversed rightward bias (Siniscalchi et al., 2016b) which would implicate that the side a dog trainer is to the dog may have an effect on their success. These effects would be consistent with the hypothesis that laterality may have functional benefits in development of motor and/or cognitive skills in animals.

5. Conclusions

Overall, our data suggest strong evidence that dog pawedness is affected by both sex and age, with paw preference significantly differing as dogs progress into old age. Age has not previously been found to be significantly associated with dog pawedness. Although we recognise the limits of the data collection, we believe that this study, given the large sample size, lays a foundation for future research into efficient training of dogs of differing ages and if there is a way to assess canine cognitive decline using pawedness.

Declaration of Competing Interest

The authors report no declarations of interest.

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References

Agcaoglu, O., Miller, R., Mayer, A.R., Hugdahl, K., Calhoun, V.D., 2015. Lateralization of resting state networks and relationship to age and gender. NeuroImage 104, 310–325.

Andics, A., Gácsi, M., Faragó, T., Kis, A., Miklósi, A., 2014. Voice-sensitive regions in the dog and human brain are revealed by comparative fMRI. Curr. Biol. 24, 574–578. https://doi.org/10.1016/j.cub.2014.01.058.

Andics, A., Gábor, A., Gácsi, M., Faragó, T., Szabó, D., Miklósi, A., 2016. Neural mechanisms for lexical processing in dogs. Science 353, 1030–1032. https://doi.org/10.1126/science.aaf3777.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Batt, L.S., Batt, M.S., McGreevy, P.D., 2007. Two tests for motor laterality in dogs. J. Vet. Behav. 2, 47–51. https://doi.org/10.1016/j.jveb.2007.01.002.

Batt, L.S., Batt, M.S., Baguley, J.A., McGreevy, P.D., 2008. Factors associated with success in guide dog training. J. Vet. Behav. 3, 143–151. https://doi.org/10.1016/j.jveb.2008.04.003.

BBC, 2004. 'Test Your Pet' [Measurement Instrument]. Retrieved from. http://www.bbc.co.uk/sn/tvradio/programmes/testyourpet/.

Bell, A.T., Niven, J.E., 2016. Strength of forelimb lateralisation predicts motor errors in an insect. Biol. Lett. 12 https://doi.org/10.1098/rsbl.2016.0547, 20160547.

Branson, N.J., Rogers, L.J., 2006. Relationship between paw preference strength and noise phobia in *Canis familiaris*. J. Comp. Psychol. 120, 176–183. https://doi.org/10.1037/0735-7036.120.3.176.

Burgess, J.W., Villablanca, J.R., 1986. Recovery of function after neonatal or adult hemispherectomy in cats. II. Limb bias and development, paw usage, locomotion and rehabilitative effects of exercise. Behav. Brain Res. 20 (1), 1–17. https://doi.org/10.1016/0166-4328(86)90096-3.

Cherbuin, N., Sachdev, P.S., Anstey, K.J., 2011. Mixed handedness is associated with greater age-related decline in volumes of the hippocampus and amygdala: the PATH through life study. Brain Behav. 1, 125–134. https://doi.org/10.1002/brb3.24.

Clarke, T., Mills, D.S., Cooper, J.J., 2019. Exploring the utility of traditional breed group classification as an explanation of problem-solving behavior of the domestic dog (*Canis familiaris*). J. Vet. Behav. 33, 103–107. https://doi.org/10.1016/j.jveb.2019.06.004.

Crawley, M.J., 2005. Statistics: an Introduction Using R. John Wiley & Sons.

Epstein, M., Kuehn, N., Landsberg, G., 2005. AAHA senior care guidelines for dogs and cats. J. Am. Anim. Hosp. Assoc. 41, 81–91. https://doi.org/10.5326/0410081.

Frasnelli, E., 2013. Brain and behavioural lateralisation in invertebrates. Front. Psychol. 4, 939. https://doi.org/10.3389/fpsyg.2013.00939.

Hirnstein, M., Hugdahl, K., Hausmann, M., 2019. Cognitive sex differences and hemispheric asymmetry: a critical review of 40 years of research. Laterality Asymmetries Body Brain Cogn. 24, 204–252. https://doi.org/10.1080/1357650X.2018.1497044.

Landsberg, G., Hunthausen, W., Ackerman, L., 2003. The effects of aging on the behaviour of senior pets. In: Landsberg, G., Hunthausen, W., Ackerman, L. (Eds.), Handbook of Behaviour Problems of the Dog and Cat, 2nd ed. Saunders, Edinburgh, UK, pp. 269–304.

MacNeilage, P.F., Studdert-Kennedy, M.G., Lindblom, B., 1987. Primate handedness reconsidered. Behav. Brain Sci. 10, 247–263. https://doi.org/10.1017/S0140525X00047695.

Marshall-Pescini, S., Barnard, S., Branson, N.J., Valsecchi, P., 2013. The effect of preferential paw usage on dogs' (*Canis familiaris*) performance in a manipulative problem-solving task. Behav. Processes 100, 40–43. https://doi.org/10.1016/j.beproc.2013.07.017.

McDowell, L.J., Wells, D.L., Hepper, P.G., 2018. Lateralisation of spontaneous behaviours in the domestic cat, *Felis silvestris*. Anim. Behav. 135, 37–43. https://doi.org/10.1016/j.anbehav.2017.11.002.

McGreevy, P.D., Brueckner, A., Thomson, P.C., Branson, N.J., 2010. Motor laterality in 4 breeds of dog. J. Vet. Behav. Clin. Appl. Res. 5, 318–323. https://doi.org/10.1016/j.jveb.2010.05.001.

McGrew, W.C., Marchant, L.F., 1999. Laterality of hand use pays off in foraging success for wild chimpanzees. Primates 40, 509–513. https://doi.org/10.1007/BF02557586.

Milgram, N.W., 2003. Cognitive experience and its effect on age-dependent cognitive decline in beagle dogs. Neurochem. Res. 28, 1677–1682. https://doi.org/10.1023/A:1026009005108.

Ocklenburg, S., Güntürkün, O., 2017. The Lateralized Brain: the Neuroscience and Evolution of Hemispheric Asymmetries. Academic Press, London, England.

Ocklenburg, S., Isparta, S., Peterburs, J., Papadatou-Pastou, M., 2019. Paw preferences in cats and dogs: meta-analysis. Laterality Asymmetries Body Brain Cogn. 24, 647–677. https://doi.org/10.1080/1357650X.2019.1578228.

Papadatou-Pastou, M., Ntolka, E., Schmitz, J., Martin, M., Munafò, M.R., Ocklenburg, S., Paracchini, S., 2020. Human handedness: a meta-analysis. Psychol. Bull. 146, 481–524. https://doi.org/10.1037/bul0000229.

Poyser, F., Caldwell, C., Cobb, M., 2006. Dog paw preference shows liability and sex differences. Behav. Processes 73, 216–221. https://doi.org/10.1016/j.beproc.2006.05.011.

Quaranta, A., Siniscalchi, M., Frate, A., Vallortigara, G., 2004. Paw preference in dogs: relations between lateralised behaviour and immunity. Behav. Brain Res. 153, 521–525. https://doi.org/10.1016/j.bbr.2004.01.009.

Quaranta, A., Siniscalchi, M., Vallortigara, G., 2007. Asymmetric tail-wagging responses by dogs to different emotive stimuli. Curr. Biol. 17, 199–201. https://doi.org/10.1016/j.cub.2007.02.008.

Ratcliffe, V.F., Reby, D., 2014. Orienting asymmetries in dogs' responses to different communicatory components of human speech. Curr. Biol. 24, 2908–2912. https://doi.org/10.1016/j.cub.2014.10.030.

Regaiolli, B., Mancini, L., Vallortigara, G., Spiezio, C., 2020. Paw preference in wolves (*Canis lupus*): a preliminary study using manipulative tasks. Laterality Asymmetries Body Brain Cogn. https://doi.org/10.1080/1357650X.2020.1853763.

Reinholz-Trojan, A., Włodarczyk, E., Trojan, M., Kulczynski, A., Stefanska, J., 2012. Hemispheric specialization in domestic dogs (*Canis familiaris*) for processing different types of acoustic stimuli. Behav. Processes 91, 202–205. https://doi.org/10.1016/j.beproc.2012.07.001.

Rogers, L.J., Vallortigara, G., Andrew, R.J., 2013. Divided Brains: the Biology and Behaviour of Brain Asymmetries. Cambridge University Press.

Sánchez-Vizcaíno, F., Noble, P.M., Jones, P.H., Menacere, T., Buchan, I., Reynolds, S., Dawson, S., Gaskell, R.M., Everitt, S., Radford, A.D., 2017. Demographics of dogs, cats, and rabbits attending veterinary practices in Great Britain as recorded in their electronic health records. BMC Vet. Res. 13, 218. https://doi.org/10.1186/s12917-017-1138-9.

Schneider, L.A., Delfabbro, P.H., Burns, N.R., 2013. Temperament and lateralisation in the domestic dog (*Canis familiaris*). J. Vet. Behav. 8, 124–134. https://doi.org/10.1016/j.jveb.2012.06.004.

Siniscalchi, M., Quaranta, A., Rogers, L.J., 2008. Hemispheric specialization in dogs for processing different acoustic stimuli. PLoSOne 3, 3349. https://doi.org/10.1371/journal.pone.0003349.

Siniscalchi, M., Sasso, R., Pepe, A.M., Vallortigara, G., Quaranta, A., 2010. Dogs turn left to emotional stimuli. Behav. Brain Res. 208, 516–521. https://doi.org/10.1016/j.bbr.2009.12.042.

Siniscalchi, M., Sasso, R., Pepe, A.M., Dimatteo, S., Vallortigara, G., Quaranta, A., 2011. Sniffing with right nostril: lateralisation of response to odour stimuli by dogs. Anim. Behav. 82, 399–404. https://doi.org/10.1016/j.anbehav.2011.05.020.

Siniscalchi, M., Bertino, D., Quaranta, A., 2014. Laterality and performance of agility trained dogs. Laterality Asymmetries Body Brain Cogn. 19, 219–234. https://doi.org/10.1080/1357650X.2013.794815.

Siniscalchi, M., d'Ingeo, S., Quaranta, A., 2016a. The dog nose "KNOWS" fear: asymmetric nostril use during sniffing at canine and human emotional stimuli. Behav. Brain Res. 304, 34–41. https://doi.org/10.1016/j.bbr.2016.02.011.

Siniscalchi, M., d'Ingeo, S., Fornelli, S., Quaranta, A., 2016b. Relationship between visuospatial attention and paw preference in dogs. Sci. Rep. 6 (31682) https://doi.org/10.1038/srep31682.

Siniscalchi, M., d'Ingeo, S., Quaranta, A., 2017. Lateralized functions in the dog brain. Symmetry 9, 71. https://doi.org/10.3390/sym9050071.

Szabó, D., Gee, N.R., Miklósi, Á., 2016. Natural or pathologic? Discrepancies in the study of behavioral and cognitive signs in aging family dogs. J. Vet. Behav. Clin. Appl. Res. 11, 86–98. https://doi.org/10.1038/s41598-020-74310-7.

Tan, Ü., 1987. Paw preferences in dogs. Int. J. Neurosci. 32, 825–829. https://doi.org/10.3109/00207458709043336.

Tomkins, L.M., Thomson, P.C., McGreevy, P.D., 2012. Associations between motor, sensory and structural lateralisation and guide dog success. Vet. J. 192, 359–367. https://doi.org/10.1016/j.tvjl.2011.09.010.

Van Alphen, A., Bosse, T., Frank, I., Jonker, C.M., Koeman, F., 2005. Paw preference correlates to task performance in dogs. 27th Annual Conference of the Cognitive Science Society: Cognitive Science Society, Stresa, Italy 2248–2253. Retrieved from: https://www.cs.vu.nl/~tbosse/papers/cogsci649-alphen.pdf.

Versace, E., Vallortigara, G., 2015. Forelimb preferences in human beings and other species: multiple models for testing hypotheses on lateralisation. Front. Psychol. 6, 233. https://doi.org/10.3389/fpsyg.2015.00233.

Wells, D.L., 2003. Lateralised behaviour in the domestic dog, *Canis familiaris*. Behav. Processes 61, 27–35. https://doi.org/10.1016/S0376-6357(02)00161-4.

Wells, D.L., 2020. Paw preference as a tool for assessing emotional functioning and well-being in domestic dogs and cats: a review. Appl. Anim. Behav. Sci. https://doi.org/10.1016/j.applanim.2020.105148.

Wells, D.L., Millsopp, S., 2012. The ontogenesis of lateralized behavior in the domestic cat, *Felis silvestris catus*. J. Comp. Psychol. 126 (1), 23–30. https://doi.org/10.1037/a0026522.

Wells, D.L., Hepper, P.G., Milligan, A.D.S., Barnard, S., 2017. Cognitive bias and paw preference in the domestic dog, *Canis familiaris*. J. Comp. Psychol. 131, 317–325. https://doi.org/10.1037/com0000080.

Wells, D.L., Hepper, P.G., Milligan, A.D.S., Barnard, S., 2018. Stability of motor bias inthe domestic dog, *Canis familiaris*. Behavioural Process 149, 1–7. https://doi.org/10.1016/j.beproc.2018.01.012.

Wells, D.L., Hepper, P.G., Milligan, A.D.S., Barnard, S., 2019. Lack of association between paw preference and behaviour problems in the domestic dog, *Canis familiaris*. Appl. Anim. Behav. Sci. 210, 81–87. https://doi.org/10.1016/j.applanim.2018.10.008.

Wongsaengchan, C., McKeegan, D.E.F., 2019. The views of the UK public towards routine neutering of dogs and cats. Animals 9 (138). https://doi.org/10.3390/ani9040138.