Journal of Veterinary Behavior (2012) 7, 70-79

ELSEVIER

Journal of Veterinary Behavior
Clinical Applications and Research

RESEARCH

Lateralization in the domestic dog (*Canis familiaris*): Relationships between structural, motor, and sensory laterality

L. M. Tomkins[a], K. A. Williams[b], P. C. Thomson[a], P. D. McGreevy[a]

[a]*Faculty of Veterinary Science, University of Sydney, NSW, Australia; and*
[b]*SCUZ Technologies, Sydney, Australia.*

KEYWORDS:
hair whorls;
motor laterality;
sensory laterality;
paw preference;
dog

Abstract Several studies have assessed different components of lateralization. To date, the relationships between the 3 measures of laterality, structural, motor, and sensory, have not widely been assessed. Specifically, the relationships between structural (hair whorl characteristics) and motor or sensory lateralization have largely been overlooked. This study investigated the associations between these measures of lateralization in dogs (n = 114), using hair whorl characteristics (structural), the Kong and First-stepping Tests (motor), and the Sensory Jump Test (sensory). Several associations emerged, revealing the first evidence of a relationship between structural asymmetry (both the presence and direction of a hair whorl in various regions of the body) and sensory lateralization. Specifically, the presence of a whorl on the dog's left side of the head (cephalic) and thorax was associated with a right visual bias. In addition, right visual bias was probable if the ventral mandibular whorl was present in a counter-clockwise direction ($P = 0.008$). Our data also demonstrated an association between structural and motor laterality (paw preference). Most notably, dogs with clockwise chest whorls were significantly more right-preferent in the First-stepping Test than those with counter-clockwise whorls ($P = 0.010$). In addition, an association between measures of motor and sensory lateralization also emerged, representing some of the first evidence of such a relationship in nonhuman animals.

Introduction

Hemispheric lateralization refers to the specialized functions of the left and right sides of the brain, which result in observable differences in the use of the left and right sides of the body for both motor and sensory tasks (Vallortigara et al., 1998). Lateralization is no longer thought to be unique to humans, but instead is considered a characteristic of most vertebrates (Rogers and Andrew, 2002), with the right hemisphere primarily controlling rapid responses, while the left controls considered responses (Rogers, 2002). Possessing a lateralized brain offers several advantages at both the individual and population level, and in particular, in nondomesticated animals. At the individual level, enhanced performance and faster responses are seen in lateralized compared with nonlateralized subjects, regardless of the direction of laterality (Rogers, 2002). At the population level, the extent to which a group is

None of the authors of this article have a financial or personal relationship with other people or organizations that could inappropriately influence or bias the content of the article.

Address for reprint requests and correspondence: L.M. Tomkins, BAgSc (Hons), PhD, R.M.C. Gunn Building (B19), Faculty of Veterinary Science, University of Sydney, NSW, Australia; Tel: +61-402-123-863; Fax: +612-8002-4030.

E-mail: tomkins@optushome.com.au

1558-7878/$ - see front matter
doi:10.1016/j.jveb.2011.07.001

lateralized in the same direction can assist with survival because of both intraspecific social behavior and avoidance of predation (Rogers, 2000).

The extent to which lateralization influences the lives of companion animals is continuing to be explored. Dogs play an important role in society, both as companions and as workers. By convention, service dogs such as guide dogs are left-heel trained, and as such are required to work on the left side of their handler. This convention may prove to be a disadvantage to dogs that are less flexible when turning right, and may result in their being disqualified erroneously from training. Potentially, less flexible right-turning dogs may turn out to be just as suitable for guiding work if trained on the right side of their handler.

Visual biases may also influence suitability of dogs for work if they are particularly reliant on their right field of vision and corresponding brain hemisphere, which is often obscured by the handler when undertaking left-heel work. This bias has been reported in guide dogs where left visually preferent dogs were more successful in the Guide Dog Training Program than right visually preferent animals (Tomkins et al., 2011).

In comparison with motor and sensory lateralization, structural lateralization has received very little scientific attention. Structural asymmetries are evident in the positioning of some internal organs, such as the heart. Hair whorls, anatomical features of the hair coat that can show left-right asymmetry, are also of interest as a structural marker of lateralization (Jansen et al., 2007; Tomkins and McGreevy, 2010a,b) since the nervous system and the integument have common origins in the structure of the embryo (Smith and Gong, 1973). Given that whorls are not influenced by maturation or human intervention, they could potentially provide an external indicator of functional brain lateralization. In addition, some whorl characteristics (presence and direction) are binary outcomes, unlike motor and sensory measures that can result in animals being classified as right preferent, left preferent, or ambidextrous; thus, hair whorls may offer a more compelling tool for determining lateralization in animals.

Given that significant resources are involved in training service dogs such as police and guide dogs, determining early predictors of success is attractive to industry stakeholders. Measures of laterality, such as hair whorls, may reliably indicate suitability among dogs intended for work. An association between hair whorl characteristics and behavioral tendencies in the dog has been reported (Tomkins and McGreevy, 2010a; Tomkins et al., 2011), which has largely been focused on the chest whorl. In our preliminary study assessing hair whorl characteristics in dogs (n = 120) of various breeds and cross-breeds, the source of the dog (shelter or nonshelter) was marginally associated with the position of the chest whorl (Tomkins and McGreevy, 2010a). Dogs sourced from a shelter had a tendency for their chest whorls to be positioned further away from the thoracic inlet than nonshelter dogs. Given behavioral reasons are known to be the leading cause of relinquishment of dogs to shelters (Salman et al., 2000), it seems plausible that an association between chest whorl position and behavior exists. Furthermore, hair whorls were assessed in potential guide dogs (n = 114), and the direction of a chest whorl was found to be significantly associated with the success of a dog in the Guide Dog Training Program, where dogs with a counter-clockwise (CC) chest whorl had a higher probability of success than dogs with a clockwise (C) whorl (Tomkins et al., 2011).

Very few animal studies have compared hair whorls with other laterality measures such as motor lateralization. Murphy and Arkins (2004, 2005, 2008) investigated the relationship between cephalic hair whorls and motor laterality in the horse. The authors reported that foals with C whorls presented their right foreleg initially at birth (Murphy and Arkins, 2005); and, that, left-lateralized horses exhibited significantly more CC whorls, whereas right-lateralized horses had more C whorls than expected by chance (Murphy and Arkins, 2004, 2008). Although a significant relationship was reported by Murphy and Arkins, to the best of our knowledge, no studies have made a comparison between noncephalic hair whorls and measures of laterality. Furthermore, only limited literature is available on canine hair whorl characteristics (Tomkins and McGreevy, 2010a,b; Tomkins et al., 2011).

Studies have demonstrated that hair whorl characteristics are associated with behavioral tendencies (cattle: Grandin et al., 1995; Randle, 1998; Lanier et al., 2001; horses: Górecka et al., 2006; dogs: Tomkins and McGreevy, 2010a; Tomkins et al., 2011). A review of the literature revealed that there is a dearth of comparable data on different measures of lateralization, especially those reflecting structural lateralization. Therefore, the primary aim of this study was to compare this measure of structural lateralization with both motor and sensory laterality measures. In addition, the relationship between motor and sensory lateralization was assessed. For our study these comparisons were made in dogs, a species in which hair whorls (at 11 different regions) have been reported as a structural marker of lateralization, motor lateralization can be determined using 2 different tests (Kong and First-stepping Tests), and sensory lateralization in the form of visual bias can be determined using the Sensory Jump Test (5 measures used). The presence and direction of hair whorls were assessed for structural lateralization, while direction and strength of lateralization were measured for both motor and sensory lateralization. Direction of lateralization indicates the direction of bias (either left or right preference), whereas strength of lateralization captures asymmetry in the activity of the 2 appendages (paws for motor laterality) or organs (eyes for sensory laterality), without taking into account the direction of the preference.

Methods and materials

Animals

Dogs participating in the laterality study were aged between 13 and 17 months, and sourced from Guide Dogs NSW/ACT. The cohort of trainee guide dogs (n = 114) were all neutered (males, n = 53; females, n = 61), and included Labrador retrievers (n = 97), golden retrievers (n = 9), and Labrador–golden retriever crosses (n = 8). Although the full cohort (n = 114) of dogs participated in the Kong Test (motor lateralization) and hair whorl assessments, only a portion of these dogs were assessed in the First-stepping Test (n = 113; males, n = 52; females, n = 61) and for sensory lateralization (n = 76; males, n = 34; females, n = 42). Dogs entered the training facility in groups (group 1, n = 19; group 2, n = 24; group 3, n = 30; group 4, n = 16; group 5, n = 25), approximately 3 months apart. All laterality assessments were conducted at the Guide Dogs NSW/ACT Training Centre in Glossodia, New South Wales, Australia. All dogs undergoing laterality assessments were assessed by a veterinarian and ophthalmologist to ensure that no underlying conditions were present that may have influenced their performance in the study. The protocols in this study were approved by the Animal Ethics Committee of the University of Sydney, Sydney, Australia (approval number N00/1-2008/3/4759).

Structural lateralization—hair whorl assessment

A palpation and hair-cluster method of assessment, as described by Tomkins and McGreevy (2010a,b), was used to classify hair whorl characteristics in the dogs. Hair whorls were assessed in 11 different regions of the dog's body (see Tables 1 and 2), and whorls could occur centrally (e.g., chest and ventral mandibular) or bilaterally (e.g., brachial axillary and elbows). Whorls were classified as simple or tufted, based on whether the hair diverges from (simple), or converges to (tufted), a single focal point (epicenter). Within each of the regions assessed, the direction in which hair rotates around this epicenter was determined as clockwise (C) or counter-clockwise (CC).

Motor lateralization—paw preference

Paw preference was determined by following the methodology outlined in the study performed by Tomkins et al. (2010a), using both the Kong and First-stepping Tests. Briefly, 50 left- or right-paw uses were recorded for each dog and for each test; the Kong Test being a food-retrieval task (paw used to hold the food-filled Kong), and the First-stepping Test reflecting locomotory behavior (first paw used to step-off a 3-step wooden staircase). Paw preference was determined using the lateralization index (LI: $[R - L]/[R + L] \times 100$; where R = number of right paw uses; L = number of left paw uses, such that negative LI values represented left lateral biases). Lateral strength was determined by the absolute value of LI.

Sensory lateralization—visual bias

Visual biases were determined using the Sensory Jump Test, as described in the study performed by Tomkins et al. (2010b). Briefly, 3 different ocular treatments (binocular vision, right monocular vision [RMV], and left monocular vision [LMV]) were created using modified head halters (Halti head halters; The Company of Animals Ltd., England, UK) to assess eye preference in a jumping task. A customized light grid (SCUZ Technologies, Castle Hill, NSW, Australia) was arranged to one side of a dog agility jump to enable accurate and objective recording of jump kinematics. As defined by Tomkins et al. (2010b), a series

Table 1 Presence, classification, and direction of whorls occurring bilaterally

	Right side					Left side				
		Classification (%)		Direction (%)			Classification (%)		Direction (%)	
Position	Presence (%)	Simple	Tufted	C	CC	Presence (%)	Simple	Tufted	C	CC
Cephalic	0.9	100.0	0.0	100.0	0.0	0.9	100.0	0.0	0.0	100.0
Cervical–dorsal	0.0	–	–	–	–	0.0	–	–	–	–
Cervical–lateral	2.6	100.0	0.0	66.7	33.3	0.9	100.0	0.0	100.0	0.0
Brachial axillae	98.3	100.0	0.0	0.0	100.0	95.6	100.0	0.0	100.0	0.0
Thoracic axillae	14.4	100.0	0.0	31.2	69.8	10.8	100.0	0.0	66.7	33.3
Shoulder	7.0	100.0	0.0	37.5	62.5	7.0	100.0	0.0	75.0	25.0
Elbow	92.1	0.0	100.0	8.6	91.4	92.1	0.0	100.0	88.6	11.4
Abdominal	0.9	100.0	0.0	100.0	0.0	1.8	100.0	0.0	0.0	100.0
Ischiatic	87.7	100.0	0.0	100.0	0.0	86.0	100.0	0.0	0.0	100.0

C, clockwise; CC, counter-clockwise.
Note: The percentage of dogs with whorls present in each region is based on n = 114, except for cephalic whorls (n = 113), and thoracic axillary whorls (n = 111).

Table 2 Presence, classification, and direction of whorls occurring centrally

		Classification (%)		Direction (%)	
Position	Presence (%)	Simple	Tufted	C	CC
Ventral mandibular	11.1	100.0	0.0	66.7	33.3
Chest	92.1	0.0	100.0	14.3	85.7

C, clockwise; CC, counter-clockwise.
Note: The percentage of dogs with whorls present in each region is based on n = 114 for chest whorls and n = 108 for ventral mandibular whorls.

of attributes for each attempted jump was recorded as follows: (i) approach distance, (ii) forepaw clearance height, (iii) hindpaw clearance height, (iv) lowest body part clearance height, and (v) jump success. Visual preference (right visual or left visual bias) was determined using a modified LI for each of the 5 aforementioned jump parameter outcomes. The formula used to assess sensory laterality was LI = ($\sum$[LMV – Bin Ave] – $\sum$[RMV – Bin Ave])/Bin Ave (where LMV = left monocular vision jump outcome, RMV = right monocular vision jump outcome, Bin Ave = binocular average jump outcome, and $\sum$ = sum of).

Statistical analysis

The analyses in this study were conducted using the statistical package GenStat, 10th edition (VSN International Ltd.; Hemel Hempstead, UK). A series of univariate restricted maximum likelihood (REML) models (n = 376) with group as a random effect were used to assess the effects of each of the predictor variables (presence and direction of a whorl in each region) on the outcome variables (the direction and strength of both motor and sensory laterality measures). REML was also used to determine any association between motor and sensory indices, where the direction and strength of motor laterality measures were used as the predictor variables, and the direction and strength of sensory laterality measures were used as outcome variables. Separate models were fitted for the strength and the direction associations. Significance was determined at a level of $P \leq 0.05$, with values between $0.05 < P < 0.1$ being marginally nonsignificant and only demonstrating a tendency towards levels of significance.

Table 3 Descriptive statistics for motor lateralization measures from both the Kong (n = 114 dogs) and First-stepping (n = 113 dogs) Tests

Laterality measure	Mean	SD	Min	Max
Kong Test				
Direction	−3.12	31.80	−68.00	80.00
Strength	25.79	18.71	0.00	80.00
First-stepping Test				
Direction	11.12	55.57	−100.00	100.00
Strength	48.64	28.74	0.00	100.00

SD, standard deviation; Min, minimum value; Max, maximum value.

Following the precedent reported in horse (Murphy and Arkins, 2004; Górecka et al., 2006), cattle (Evans et al., 2005), and dog (Tomkins and McGreevy, 2010a,b) studies, dogs that had multiple hair whorls in a single region and on a single side were recorded, but excluded from the analysis. This protocol caused the exclusion of dogs from the cephalic (n = 1), ventral mandibular (n = 6), and thoracic axillary (n = 3) whorl analyses.

Results

Hair whorl characteristics

The presence, direction, and classification of whorls that are located bilaterally or centrally can be seen in Tables 1 and 2, respectively. Briefly, in more than 10% of the dogs, whorls were present in the ventral mandibular, chest, brachial and thoracic axillary, elbow, and ischiatic regions. Whorls were uniformly classified as simple, with the exception of those on the elbows and chest, which were consistently tufted. Because of the lack of variation in simple and tufted whorl classification within a region, this aspect of hair whorl characteristics could not be analyzed to determine any potential relationships with other laterality measures. Bilateral whorls located in the cephalic, brachial axillary, abdominal, and ischiatic regions were consistent in their direction, and direction was symmetrical about the dorsal midline. Variation occurred in the direction of whorls in other regions.

Presence of whorls was analyzed at all 10 regions of the body in which whorls were located (no whorls were present in the dorsal cervical region), but analysis of the direction of the whorl was undertaken only for regions where there was variation in the direction of the whorl, and where whorls were present in more than 10% of the current sample population (n = 4; ventral mandibular, chest, elbow, and thoracic axillary regions).

Comparison between whorl characteristics and motor laterality indices

Relationship between whorl presence and motor laterality

The descriptive statistics for both the Kong and First-stepping Test measures can be seen in Table 3. The

Table 4 Descriptive statistics for sensory lateralization measures from the Sensory Jump Test (n = 76 dogs)

Laterality measure	Mean	SD	Min	Max
Jump success				
Direction	−0.31	3.20	−18.00	10.00
Strength	1.68	2.73	0.00	18.00
Approach distance				
Direction	−0.95	4.27	−23.85	7.07
Strength	2.79	3.35	−0.03	23.85
Forepaw clearance height				
Direction	−2.90	16.28	−120.00	23.75
Strength	7.54	14.69	0.00	120.00
Hindpaw clearance height				
Direction	−0.77	6.44	−22.76	14.89
Strength	4.54	4.61	0.00	22.76
Lowest body part clearance height				
Direction	−3.48	16.12	−115.00	14.44
Strength	8.42	14.16	0.00	115.00

SD, standard deviation; Min, minimum value; Max, maximum value.

direction of motor laterality (lateralization index [LI]) using the Kong Test was not significantly associated with the presence of a whorl in any of the regions assessed (all $P > 0.053$). However, the strength of motor laterality using the Kong Test was associated with the presence of both left ($P = 0.002$) and right ($P = 0.002$) elbow whorls, in that a reduction in lateral strength (|LI|) was observed with the presence of either of the elbow whorls (left or right side, whorl present [WP], |LI| = 24.19; whorl absent [WA], |LI| = 44.44).

Several significant associations were also revealed between the presence of a whorl and motor laterality, as determined using the First-stepping Test. The presence of a cephalic whorl was associated with both the direction and strength of motor laterality. Dogs that had a cephalic whorl present on the left side of their head displayed a left motor bias (WP, LI = −92.00; WA, LI = 12.97; $P = 0.008$), and were significantly more lateralized than those with no whorl (WP, |LI| = 89.82; WA, |LI| = 47.84; $P = 0.041$). A shift toward left motor bias was also observed in dogs with either a left (WP, LI = −23.69; WA, LI = 15.64; $P = 0.016$) or right (WP, LI = −16.44; WA, LI = 16.34; $P = 0.021$) thoracic axillary whorl, whereas a shift toward right motor bias was observed in dogs with a ventral mandibular whorl (WP, LI = 40.89; WA, LI = 5.47; $P = 0.013$).

Relationship between whorl direction and motor laterality

The direction of a hair whorl at several locations was associated with the direction and strength of motor laterality, as determined using the Kong and First-stepping Tests. The direction of a chest whorl was associated with the direction of motor laterality using the First-stepping Test. Dogs with C chest whorls were significantly more right-preferent in this motor laterality task than dogs with CC whorls (C, LI = 46.00; CC, LI = 4.84; $P = 0.010$). Strength of paw preference was also significantly associated with the direction of some whorls. Dogs with a clockwise left thoracic axillary whorl had a greater strength of motor bias when assessed using the First-stepping Test (C, |LI| = 70.76; CC, |LI| = 11.72; $P = 0.005$). A reduction in lateral strength, as determined using the Kong Test, was observed in dogs with clockwise ventral mandibular whorls (C, |LI| = 28.59; CC, |LI| = 59.77; $P = 0.026$).

Comparison between whorl characteristics and sensory laterality indices

Relationship between whorl presence and sensory laterality

The descriptive statistics for the Sensory Jump Test measures can be seen in Table 4. Several significant relationships were identified between the presence of hair whorls in certain locations and the direction and strength of sensory laterality measures (approach distance, forepaw clearance height, hindpaw clearance height, and lowest body part clearance height). The direction of visual bias observed when a statistically significant relationship was identified between sensory laterality measures, as determined by the Sensory Jump Test, and the presence of a hair whorl within different regions can be seen in Table 5.

The presence of whorls at any of the 10 regional locations was not associated with the sensory laterality

Table 5 Direction of visual bias observed when a statistically significant relationship was identified between sensory laterality measures, as determined by the Sensory Jump Test, and presence of a hair whorl, at different locations

	Whorl location				
Sensory Jump Test measure	Cephalic left side	Cervical right side	Shoulder left side	Thoracic axillary left side	Chest
Jump success	NS	NS	NS	NS	NS
Approach distance	NS	NS	NS	Right	NS
Forepaw clearance height	Right	NS	Right	Right	NS
Hindpaw clearance height	NS	Right	NS	NS	Left
Lowest body part clearance height	Right	NS	Right	Right	NS

NS, nonsignificant.

indices for jump success (all $P > 0.055$). However, the presence of a whorl was associated with other sensory measures including approach distance and clearance heights.

Dogs with a left cephalic whorl were significantly more likely to have a right visual bias (RVB) for both forepaw clearance height (WP, LI = −58.87; WA, LI = −1.34; $P < 0.001$), and the lowest body part clearance height (WP, LI = −58.53; WA, LI = −1.95; $P < 0.001$), than the dogs without a whorl. In addition, dogs with a left cephalic whorl were also more strongly lateralized for both of these sensory measures (forepaw clearance height: WP, |LI| = 61.12; WA, |LI| = 6.05; $P < 0.001$; lowest body part clearance height: WP, |LI| = 58.53; WA, |LI| = 7.02; $P < 0.001$) than dogs without a whorl in this region.

The presence of a right lateral cervical whorl was associated with the direction of laterality for hindpaw clearance height. Dogs with a whorl present in this region were significantly more likely to have RVB (WP, LI = −8.05; WA, LI = −0.46; $P = 0.045$) than dogs without.

Whorls present on the left and right sides of the thorax were associated with several sensory measurements, including approach distance, forepaw clearance height, and lowest body part clearance height. The direction of laterality for approach distance was associated only with the presence of left thoracic axillary whorls, where dogs with a whorl present in this region were significantly more likely to have RVB (WP, LI = −4.53; WA, LI = −0.56; $P = 0.018$) than dogs without. Presence of a left thoracic axillary whorl was also associated with both the direction and strength of forepaw clearance height. Dogs with a whorl in this region were more likely to have RVB (WP, LI = −20.89; WA, LI = −1.04; $P = 0.002$), and were more strongly lateralized (WP, |LI| = 22.15; WA, |LI| = 6.02; $P = 0.005$) than those without a left thoracic axillary whorl. Similarly, dogs with a whorl in this region were more likely to have RVB for lowest body part clearance height (WP, LI = −20.78; WA, LI = −1.68; $P = 0.002$), and were more strongly lateralized (WP, |LI| = 24.08; WA, |LI| = 6.89; $P = 0.001$) than those without a whorl. Dogs with a right thoracic whorl were more strongly lateralized for both forepaw clearance height (WP, |LI| = 15.83; WA, |LI| = 6.09; $P = 0.042$) and lowest body part clearance height (WP, |LI| = 17.60; WA, |LI| = 6.84; $P = 0.018$), than those without a whorl.

Dogs with a left shoulder whorl were significantly more likely to have RVB for forepaw clearance height (WP, LI = −41.22; WA, LI = −1.28; $P < 0.001$) and lowest body part clearance height (WP, LI = −41.11; WA, LI = −1.89; $P < 0.001$), and were more strongly lateralized for both measures (forepaw clearance height: WP, |LI| = 44.33; WA, |LI| = 5.99; $P < 0.001$; lowest body part clearance height: WP, |LI| = 43.41; WA, |LI| = 7.01; $P < 0.001$) than dogs without a whorl in this region.

The presence of a left or right brachial axillary or elbow whorl was not significantly associated with any of the sensory measures (all $P > 0.185$). The presence of a chest whorl was marginally associated with the direction of hindpaw clearance height. Dogs without a chest whorl were more likely to have RVB (WP, LI = −0.24; WA, LI = −4.56; $P = 0.059$) than those having a chest whorl.

Relationship between whorl direction and sensory laterality

The direction of a whorl in the ventral mandibular, chest, elbow, and thoracic axillary regions was not strongly associated with the sensory laterality indices for approach distance, forepaw clearance height, hindpaw clearance height, or the lowest body part clearance height (all $P > 0.066$). There was only a marginally nonsignificant relationship between the direction of a chest whorl and sensory laterality indices for hindpaw clearance height. Dogs with C chest whorls were more likely to have RVB than dogs with CC whorls (C, LI = −4.82; CC, LI = 0.14; $P = 0.078$).

In contrast, the direction of a ventral mandibular whorl was associated with the direction and strength of laterality for jump success. Dogs with a CC whorl were significantly more likely to have RVB, whereas dogs with C whorls showed a lack of a visual bias, and were more likely to be ambidextrous (C, LI = 0.00; CC, LI = −1.06; $P = 0.008$). Dogs with CC ventral mandibular whorls were also more strongly lateralized (C, |LI| = 0.00; CC, |LI| = 1.06; $P = 0.008$) than dogs with C whorls.

Summary of structural lateralization associations

The full results of the REML analyses showing significant associations between whorl characteristics, both presence and direction, and measures of motor and sensory lateralization can be seen in Table 6, whereas the relationship between these measures can be seen in Table 7.

Comparison between motor and sensory laterality indices

There was no association found between the LIs for the 5 measures of sensory lateralization and the motor LI for paw preference using the Kong Test (all $P > 0.15$). In comparison, when using the First-stepping Test, strength of motor laterality was associated with the direction of the lowest body part clearance height LI ($P = 0.042$). For each one unit increase in strength of paw preference, there was a 0.13 ± 0.07 decrease in the lowest body part clearance height LI.

Discussion

To our knowledge, this is the first study to report on the relationship between the 3 measures of laterality, that is,

Table 6 Full results of the REML analyses showing significant associations between measures of structural, and both motor, and sensory lateralization

Predictor variable	Outcome variable	Estimate	SE	*P*
Stuctural versus Motor lateralization				
Presence				
Left cephalic whorl	First-stepping (direction)	−104.970	38.560	0.008
Left cephalic whorl	First-stepping (strength)	41.980	20.300	0.041
Left thoracic axillary whorl	First-stepping (direction)	−39.330	16.030	0.016
Right thoracic axillary whorl	First-stepping (direction)	−32.780	14.010	0.021
Left elbow whorl	Kong (strength)	−20.250	6.240	0.002
Right elbow whorl	Kong (strength)	−20.250	6.240	0.002
Ventral mandibular whorl	First-stepping (direction)	35.420	13.950	0.013
Direction				
Left thoracic axillary whorl	First-stepping (strength)	59.040	16.560	0.005
Ventral mandibular whorl	Kong (strength)	−31.180	11.770	0.026
Chest whorl	First-stepping (direction)	41.160	15.620	0.010
Stuctural versus Sensory lateralization				
Presence				
Left cephalic whorl	FCH (direction)	−57.530	9.598	<0.001
	FCH (strength)	55.070	8.388	<0.001
	LBPCH (direction)	−56.580	9.537	<0.001
	LBPCH (strength)	51.510	8.219	<0.001
Left thoracic axillary whorl	AD (direction)	−3.973	1.640	0.018
	FCH (direction)	−19.848	6.047	0.002
	FCH (strength)	16.135	5.561	0.005
	LBPCH (direction)	−19.101	6.042	0.002
	LBPCH (strength)	17.187	5.196	0.001
Left shoulder whorl	FCH (direction)	−39.950	8.438	<0.001
	FCH (strength)	38.350	7.458	<0.001
	LBPCH (direction)	−39.220	8.377	<0.001
	LBPCH (strength)	36.390	7.171	<0.001
Right cervical–lateral whorl	HCH (direction)	−7.591	3.718	0.045
Right thoracic axillary whorl	FCH (strength)	9.748	4.708	0.042
Right thoracic axillary whorl	LBPCH (strength)	10.756	4.446	0.018
Direction				
Ventral mandibular whorl	JS (direction)	1.056	0.096	0.008
Ventral mandibular whorl	JS (strength)	−1.056	0.096	0.008

AD, approach distance; FCH, forepaw clearance height; HCH, hindpaw clearance height; LBPCH, lowest body part clearance height; JS, jump success; SE, standard error.

Note: Values shown as "Estimate" are estimated regression coefficients and show the average change in the outcome variable in the presence of a whorl, compared with it being absent or, the direction being clockwise, compared with counter-clockwise.

structural, motor, and sensory. Several associations were identified between structural and motor, structural and sensory, and motor and sensory lateralization.

The findings of our study support the association between structural and motor laterality measures in the horse reported by Murphy and Arkins (2004, 2008). Similar to the studies performed by Murphy and Arkins (2004, 2008) where more C whorls (cephalic) were seen on right-preferent horses, dogs with C chest whorls were significantly more right-preferent in the First-stepping motor laterality task than dogs with CC whorls. This was an interesting finding, given that we have previously reported an association between this measure of structural laterality and behavioral tendencies in the dog in terms of success in the Guide Dog Training Program (Tomkins et al., 2011). Specifically, the probability of success as a guide dog was significantly reduced when chest whorls were clockwise in direction.

Interestingly, the presence of a whorl in certain locations was also associated with motor laterality. Dogs with a ventral mandibular whorl had a significant shift towards right motor bias, whereas a shift towards left motor laterality was observed for dogs with a whorl on the left side of the head (cephalic), and on both the left and right sides of the thorax. The presence of a left cephalic whorl was also associated with a greater strength of laterality, independent of direction. It is worth emphasizing that only atypical whorls (those that occur in less than 20% of the sample population; Tomkins and McGreevy, 2010a,b) were associated with motor laterality.

Table 7 Relationship between measures of structural lateralization and measures of motor and sensory laterality

Whorl location	Side of midline	Relationship with motor and sensory measures
Cephalic	Left	Whorl present → left motor bias (FST)
		Whorl present → ↑ motor strength (FST)
		Whorl present → right visual bias (FCH, LBPCH)
		Whorl present → ↑ visual strength (FCH, LBPCH)
	Right	NS
Cervical–lateral	Left	NS
	Right	Whorl present → right visual bias (HCH)
Ventral mandibular	–	Whorl present → right motor bias (FST)
		Whorl direction (clockwise) → ↓ motor strength (KT)
		Whorl direction (counter-clockwise) → right visual bias (JS)
		Whorl direction (counter-clockwise) → ↑ visual strength (JS)
Chest	–	Whorl absent → right visual bias (HCH)
		Whorl direction (clockwise) → right motor bias (FST)
		Whorl direction (clockwise) → right visual bias (HCH)
Brachial axillary	Left	NS
	Right	NS
Thoracic axillary	Left	Whorl present → left motor bias (FST)
		Whorl present → right visual bias (AD, FCH, LBPCH)
		Whorl present → ↑ visual strength (FCH, LBPCH)
		Whorl direction (clockwise) → ↑ motor strength (FST)
	Right	Whorl present → left motor bias (FST)
		Whorl present → ↑ visual strength (FCH, LBPCH)
Elbow	Left	Whorl present → ↓motor strength (KT)
	Right	Whorl present → ↓motor strength (KT)
Shoulder	Left	Whorl present → right visual bias (FCH, LBPCH)
		Whorl present → ↑ visual strength (FCH, LBPCH)
	Right	NS
Abdomen	Left	NS
	Right	NS
Ischiatic	Left	NS
	Right	NS

FST, First-stepping Test; KT, Kong Test; AD, approach distance; FCH, forepaw clearance height; HCH, hindpaw clearance height; LBPCH, lowest body part clearance height; JS, jump success; NS, nonsignificant.

The presence of a whorl on the left side of the body on the head (cephalic), neck (cervical), shoulder, and thorax was associated with RVB for numerous Sensory Jump Test parameters, including forepaw clearance height and lowest body part clearance height. In contrast, the presence of a whorl was only associated with a left visual bias when a whorl occurred in the central location of the chest. In addition, if a ventral mandibular whorl was present, a dog was more likely to have RVB if the whorl was in CC direction. Interestingly, dogs with a C ventral mandibular whorl showed a lack of visual bias. To date, this is the first study to report associations between sensory and structural lateralization.

Previous studies in primates (Cole, 1957; Kruper et al., 1966; Rogers et al., 1994; Hook-Costigan and Rogers, 1995, 1998), horses (McGreevy and Rogers, 2005), and dogs (Tomkins et al., 2010b) have reported the absence of an association between motor and sensory laterality, suggesting that these measures occur on at least 2 different levels of neural control. However, using the First-stepping and Sensory Jump Tests, this study reports that there is an association between measures of motor and sensory lateralization, that is, as lateral strength of paw preference increased, dogs shifted toward RVB.

Many studies conducted on lateralization have reported that paw preference changes with task complexity (Fagot and Vauclair, 1991; Spinozzi and Truppa, 1999; Wells, 2003; Trouillard and Blois-Heulin, 2005; Batt et al., 2008). This may also hold true for motor and sensory tasks when different motivation and action patterns are required to perform a given task. In primates, eye preference is often determined by noting the eye that is used to look through a monocular viewing hole at the presented stimuli (ranging from innate objects, food, or a predator; Hook-Costigan and Rogers, 1998; Chapelain and Blois-Heulin, 2009; de Latude et al., 2009), and hand preference often involves reaching for an object and is based on foraging behavior (Stafford et al., 1990; Hook-Costigan and Rogers, 1995; Spinozzi and Truppa, 1999; Westergaard et al., 2003, 2004; Vauclair et al., 2005; O'Malley and McGrew, 2006). It may be that these 2 tasks require different modes of processing, whereas in our study, both the First-stepping Test (paw preference) and the Sensory Jump Test (visual preference) require analysis and processing of spatial information to navigate the task. Although in our study it was strength of one measure of laterality (e.g., strength of paw preference) that was associated with the direction of the other measure (e.g., direction of laterality for the lowest body part clearance height), the similar mechanisms required for processing may help to explain why our data have demonstrated an association between motor and sensory lateralization.

By establishing a link between hair whorls and lateralized behavior, one factor can be used as an indicator of the other. Most notably, the presence of a left cephalic or thoracic axillary whorl was associated with a left motor bias and RVB, both of which have been associated with reduced probability of success in the Guide Dog Training Program (Tomkins et al., 2011). In our previous study (Tomkins et al., 2011), a reduced probability of success as a guide was also seen for dogs with C chest whorls. In the current study, a relationship between both of these measures was associated with a lower probability of guide dog success (RVB and C chest whorls), where dogs with a C chest whorl were likely to have RVB. Dogs with a C chest whorl were also significantly more right-preferent in the First-stepping Test than those with CC whorls. Using morphological indictors of laterality may aid trainers in identifying dogs suitable for service work. In addition, the presence or direction of hair whorls may indicate lateralized behavioral tendencies in the horse, dog, and other species, thereby providing a tool for trainers when tailoring conditioning programs for individuals.

By identifying early predictors of an animal's working success, such as the aforementioned laterality measures, the efficiency with which suitable animals are selected may increase. Husbandry and training costs would decrease if unsuitable animals were removed from the training programs earlier and re-homed, while allowing trainers to better use their time on animals with a greater potential. Welfare benefits may also ensue, with unsuitable animals no longer being required to undergo training that constitutes an innate challenge to them.

Conclusion

To our knowledge, this is one of the first studies to assess all 3 measures of laterality (structural, motor, and sensory lateralization), and furthermore, the first to assess the relationship between these measures. The presence and direction of whorls in several regions were associated with motor and sensory measures. Given measures of laterality have been associated with identifying dogs suitable for working environments, morphological indictors of laterality such as hair whorls may provide a quick and efficient means of determining suitability. The identification of relationships between these 3 aforementioned measures of laterality also increases our knowledge of canine lateralization, and provides a basis for ongoing studies in applied canine ethology.

Acknowledgments

The authors thank Guide Dogs NSW/ACT for providing the facility and dogs to conduct this study. The Australian Research Council and Guide Dogs NSW/ACT provided funding for this project. The authors also thank the 2 anonymous referees whose comments on this article were greatly valued.

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