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Associations between motor, sensory and structural lateralisation and guide dog success

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ABSTRACT

The aim of this study was to determine whether objective measures of laterality could be used to identify dogs with a high probability of successfully completing a Guide Dog Training Programme. Three categories of laterality (motor, sensory, and structural), were assessed in 114 dogs entering guide dog training. Significant predictors of success were identified: the direction of laterality ($P = 0.028$), paw preference category in the 'Kong' test ($P = 0.043$), hindpaw clearance height ($P = 0.002$), laterality indices for a number of measures in the Sensory Jump test, and chest hair whorl direction ($P = 0.050$). This is the first study to report a structural marker of canine behaviour. All three categories of laterality may be used to predict the suitability of dogs for guiding work, and by identifying predictors of success, resources can be more efficiently utilised on dogs with greater potential.

Introduction

Guide dogs play an important role in society by providing independent mobility to people with visual impairment. Although guide dogs help their visually-impaired handlers to gain independence and move safely around the community, their service comes at a high cost due to the large amount of resources, both labour and financial, required to train such animals. Guide Dogs NSW/ACT (Chatswood, Australia) report that training a successful guide dog costs approximately AU$ 30,000[1] (Guide Dogs NSW/ACT, 2010). Previous studies on guide dog training have reported success rates of 50–56% for dogs in training (Ennik et al., 2006; Batt et al., 2008a). More recently, a global survey of guide dog organisations from 15 countries revealed success rates of 23–100% (Batt et al., 2010). This large variation in success may reflect different training methods and assessment criteria, the amount of time spent training, or the breeds used. Of the 174 dogs that entered the Australian NSW/ACT Guide Dog Training Programme over the last 3 years, a success rate of 49.4% was achieved, with 12.6% failing due to health and 38.5% due to behavioural problems. Therefore, identifying methods of early detection of suitability of dogs for guide work would be very beneficial in terms of reducing costs.

To date, a number of studies have assessed various aspects of guide dog training. These include genetic factors and breeding programmes (Goddard and Beilharz, 1982, 1983; Arata et al., 2007), early life experiences and puppy raising (Koda, 2001a,b; Serpell and Hsu, 2001; Batt et al., 2008a; Duffy and Serpell, 2008, 2009; Gazzano et al., 2008) and dog selection, assessment, and training (Peel, 1975; Murphy, 1995, 1998; Serpell and Hsu, 2001; Ennik et al., 2006; Duffy and Serpell, 2008; Arata et al., 2010). Many of these studies have also assessed factors that could predict the suitability of animals for guiding work (Goddard and Beilharz, 1982, 1983, 1984a, 1986; Knol et al., 1988; Serpell and Hsu, 2001; Kikkawa et al., 2005; Arata et al., 2007; Batt et al., 2008a,b; Duffy and Serpell, 2008).

A number of important findings arose from such studies. These included fearfulness, dog distraction and excitability were found to be leading behavioural reasons for failure (Goddard and Beilharz, 1982, 1984b); purpose-bred dogs had a higher success rate than donated dogs (Goddard and Beilharz, 1982, 1983); the canine behavioural assessment and research questionnaire (C-BARQ) identified a number of behavioural factors associated with success and failure including stranger-directed aggression and non-social fear (Duffy and Serpell, 2008); and temperament was associated with success in that the absence of 'pulling' in response to an unfamiliar dog increased success rates (Batt et al., 2008b). Furthermore, motor laterality findings demonstrated that a lower rate of both paws used to steady a 'Kong' while retrieving food was associated with increased success (Batt et al., 2008b), while low salivary immunoglobulin A concentrations were associated with rejection from the training programme (Kikkawa et al., 2005). Despite several studies, however, a highly accurate method of predicting success in guide dog training remains elusive. This present work evaluates objective measures of laterality to assess the suitability of dogs for guiding work.

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The specialised functions of the right and left cerebral hemispheres (otherwise known as functional lateralisation) control both motor and sensory responses. Associations between lateralised brain activity and emotional behaviour have been reported (Davidson, 1992; Hauser, 1993; Hopkins and Bennett, 1994; Hook-Costigan and Rogers, 1998; Cameron and Rogers, 1999; Larose et al., 2006). The right hemisphere (left-preferent) is associated with fearfulness, as manifested by withdrawal from novel situations and objects. In contrast, the left hemisphere (right-preferent) seems to inhibit fear, and is associated with exploration and approach of novel objects and unfamiliar environments.

Branson and Rogers (2006) reported an association between motor laterality and noise sensitivity in dogs, where the absence of a significant paw preference (in a food-retrieval task) was associated with noise-related fearfulness. Concurring with these findings, Batt et al. (2008b) reported a negative correlation between the strength of laterality and the latency of the dog to approach an unfamiliar human, to rest, and to recover from loud noises (e.g. the dropping of a metal plate on the ground).

One of the main reasons for potential guide dogs to fail in training is fearfulness, including noise sensitivity (Goddard and Beilharz, 1984b). Since the suitability of working dogs is often based on the behavioural tendencies of the dogs, the relationship between these variables is of interest in any exploration of whether laterality may be used as a predictor of suitability of dogs for specialised work. Batt et al. (2008b) assessed the ability to predict guide dog success using a test of motor laterality, the 'Kong test'. The authors reported that a lower rate of both paws being used simultaneously to 'hold' the Kong, was associated with success in the training programme. However, the use of both paws was determined (post hoc) by reviewing video footage after testing. Frequently, both of the dogs' paws are not visible in video footage captured from a stationary tripod, so only limited calculations can be made on the use of both paws from video evidence. These missing data could potentially compromise the results. The need for standardisation of motor lateralisation measures between studies has been highlighted previously (Tomkins et al., 2010a). Our study aimed to expand upon these findings by assessing a larger number of dogs and by recording both paw uses during testing.

Guiding the visually impaired demands precise and accurate movements by guide dogs and, as such, visual perception by the dog is paramount. Visual biases may therefore affect the suitability of dogs for guiding work. Given that guide dogs are generally required to work on the left side of their handler (as is the global convention in dog handling), the vision on their right side may be partially obscured. This may interfere with the dog's working ability if the dog is reliant on this field of vision and corresponding brain hemisphere. Our novel Sensory Jump test (Tomkins et al., 2010c) requires dogs to complete a series of agility jumps under three different ocular treatments: right and left monocular, and binocular vision. The resultant jump kinematics reflect the dogs' visual biases.

Whorls are a feature of a dog's hair-coat and provide a visual indicator of structural lateralisation. The association between whorls and brain development reflects a common embryonic ectodermal origin shared by the integument and nervous system (Smith and Gong, 1974). A number of studies in cattle and horses have reported an association between hair whorl characteristics and behaviour (Grandin et al., 1995; Randle, 1998; Lanier et al., 2001; Górecka et al., 2006), and laterality (Murphy and Arkins, 2004, 2005, 2008). Our pilot studies in dogs (n = 120) indicated a potential association between hair whorl characteristics (presence, direction, and position) and behavioural tendencies (Tomkins and McGreevy, 2010a,b). Most notably, 'shelter' dogs, often relinquished as a result of unfavourable behavioural attributes (Salman et al., 2000), had chest whorls that tended to be positioned further away from the thoracic inlet than non-shelter dogs. Knowing a given animal's hair whorl characteristics, and hence laterality, may facilitate predictions of its suitability to work as a guide.

The present study sought to assess whether (1) motor lateralisation (Kong and First-stepping tests), (2) sensory lateralisation (Sensory Jump test), or (3) structural lateralisation (hair whorl characteristics) could be used as a predictor of success for dogs in the Guide Dog Training Programme. We generated several hypotheses from the findings of previous studies. Firstly, the absence of significant paw preference (ambidextrous) is reported to be associated with noise-related fearfulness, and withdrawal from novel situations and objects was associated with left-preferent animals (Branson and Rogers, 2006; Larose et al., 2006; Robins and Phillips, 2010). Therefore, it was hypothesised that right-preferent animals would be more successful in guide dog training than left-preferent or ambidextrous dogs.

Secondly, analysis of spatial information is reported to be mediated through the animal's left eye, and hence perception of such information is a specialisation of the right hemisphere (Westin, 1998; Rogers, 2002; Gagliardo et al., 2005). It was thus hypothesised that visually left-preferent animals would have a higher success rate in guide dog training. Finally, cattle and horses with a cephalic hair whorl located below the eyes were calmer than those with whorls in a 'higher' position (Barker, 1990; Grandin et al., 1995; Randle, 1998; Lanier et al., 2001; Górecka et al., 2007). Dogs do not possess a central cephalic whorl, but the central chest whorl (present in >90% of dogs) shares some similarities to the cephalic whorls of cattle and horses. Therefore, it was hypothesised that dogs with chest whorls closest to the thoracic inlet would have a higher success rate in guide dog training. By identifying early predictors of success and failure, unsuitable animals could be removed from training, and time and resources can be used more efficiently on dogs that have greater potential.

Materials and methods

Animal selection

Potential guide dogs (n = 114) were assessed at the NSW/ACT Guide Dog Training Centre, Glossodia, New South Wales, Australia. Dogs participating in this study were aged between 13 and 17 months, and were all neutered (53 males, 61 females). Breeds comprised Labrador retrievers (LR) (n = 97), Golden retrievers (GR) (n = 9) and Labrador–Golden retriever crosses (LR × GR) (n = 8). Although all 114 dogs participated in the Kong test (motor lateralisation) and hair whorl assessments (structural lateralisation), 99% were assessed in the First-stepping test (n = 113; 52 males, 61 females). Due to logistical constraints and the habituation time required, only 67% of the dogs (n = 76; 34 males, 42 females) were assessed for sensory lateralisation.

Dogs entered the training facility in one of five 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 dogs undergoing laterality assessments were assessed by a veterinarian and ophthalmologist to eliminate any underlying conditions that could influence their participation in the study. This resulted in the exclusion of 14 dogs (12.3%) from the motor (Kong test) and structural lateralisation analyses, 14 dogs (12.4%) from the motor (First-stepping test) lateralisation analyses, and two dogs (2.6%) from the sensory lateralisation analysis.

The study protocols were approved by the University of Sydney's Animal Ethics Committee (approval number N00/1-2008/3/4759).

Assessment of motor lateralisation

Paw preference was determined in dogs following the methodology outlined in Tomkins et al. (2010b), 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 based on a food retrieval task, and the First-stepping test on locomotory behaviour. The occurrence of using both paws simultaneously to either hold the Kong, or to step-off by means of jumping (First-stepping) was also recorded.

Paw preference was determined using the lateralisation index (LI):

$$LI = [R - L]/[R + L] \times 100$$

where R is the number of right paw uses, L the number of left paw uses, and a left lateral biased response was represented by negative LI values.

Lateral strength was determined by the absolute value of LI.

Assessment of sensory lateralisation

Visual biases were determined using the Sensory Jump test (SJT), as described by Tomkins et al. (2010c). Briefly, three different ocular treatments (binocular vision [Bin], right monocular [RMV], and left monocular [LMV] vision), were created using modified head halters (Halti head halters, The Company of Animals Ltd.) to assess eye preference in a jumping task. A customised light grid (SCUZ Technologies) was attached to a dog agility jump to enable accurate, objective jump kinematics to be recorded.

As defined by Tomkins et al. (2010c), the four measures of interest from the light grid data were: (1) 'approach distance', the horizontal distance between the base of the jump and the launching paw; (2) 'forepaw clearance height', the vertical distance between the dorsum of the lowest forepaw and the jump bar; (3) 'hindpaw clearance height', the vertical distance between the hindpaw held lowest while jumping over the bar and jump bar; and (4) 'lowest body part clearance height', the distance between the lowest part of the body to register on the light grid and the jump bar.

Other measurements of interest included: (1) 'jump success', whether or not the dog successfully cleared the jump without knocking the bar from the jump cups; (2) 'launch paw', the last forelimb paw to touch the ground before jumping; and (3) the wither height of the dog.

Each of the 76 dogs was required to complete 10 jumps for each of the three different ocular treatments. A computer-generated list of random numbers was used to determine the order of ocular treatments for the jump. Similar to motor laterality, a LI for each of the five jump parameter outcomes (jump success, approach distance, forepaw clearance height, hindpaw clearance height, and lowest body part clearance height) was used to determine eye preference. Here, the formula used to calculate LI was modified to take into account binocular jump outcomes:

$$\mathrm{LI} = \left(\sum[\mathrm{LMV} - \mathrm{Bin\ ave}] - \sum[\mathrm{RMV} - \mathrm{Bin\ ave}]\right)/\mathrm{Bin\ ave}$$

where LMV is the left monocular vision jump outcome, RMV the right monocular vision jump outcome, and Bin ave the binocular average jump outcome.

A positive LI indicated that the dog had a left monocular bias, while negative values indicated a right monocular bias, and dogs with a LI of zero were classed as ambidextrous. Only the 10 jumps for the binocular vision were averaged (Bin ave). As the formula shows, following the subtraction of the binocular vision average from each of the 10 LMV counts, the ten values were added. This was also carried out on the RMV outcomes.

Assessment of structural lateralisation

A palpation and hair-cluster method of assessment (Tomkins and McGreevy, 2010a,b), was used to classify hair whorl characteristics in all 114 dogs. Briefly, hair whorls were assessed in 11 different regions of the dog's body. For each of these regions, whorls were classified as simple (hair diverges from a single focal point) or tufted (hair converges to a single focal point). Direction was determined as clockwise or counter-clockwise, and position was recorded as the distance between the centre of the spiral whorl and bony landmarks within each of the regions assessed.

Determining success and failure in training

At approximately 14 months of age, potential guide dog pups returned from their puppy-raising homes to the training centre where they underwent a range of tests to determine if they were physically and behaviourally suited to guide dog training. Physical examination of the dogs included radiography of the hip and elbows, and assessment of their eyes by a veterinary ophthalmologist. Initial behavioural assessments included the dog's ability to walk on a lead, to concentrate, to show low reactivity to other dogs, animals, and noises, and to cope with kennelling. It was during this initial assessment period that we conducted the laterality tests.

All tests were conducted by one of the authors (LT), with the results kept confidential until study completion. Dogs that met the above criteria were accepted and deemed suitable to commence the 20 week Guide Dog Training Programme (GDTP). Upon the completion of the 20 week programme, dogs remaining in the class graduated and were considered 'successful', in that they could be placed with a visually impaired client and commence work as a guide dog.

Dogs could be rejected at any stage throughout the training period for a variety of reasons relating to health (e.g. hip, elbow and retinal dysplasia) or behaviour (e.g. dog distraction, anxiety, excitability). The percentage of successful dogs was based on the number of dogs that graduated as a proportion of the pups that returned to training centre from puppy-walking to commence their assessments. Although laterality measures were still assessed, dogs that failed on health grounds were removed from the analyses, as the laterality tests were designed to predict associations with behavioural tendencies, and hence suitability for guiding work, not for identifying health problems.

Statistical analysis

Both the direction (LI) and strength (|LI|) of motor and sensory laterality measures were analysed. The category of paw preference and the number of both paw uses in the motor laterality studies were also assessed to determine if they could predict success in training. For structural laterality, presence, direction, and position of hair whorls were analysed. The presence of a whorl was assessed at all 10 regions in which whorls were located (no whorls were located in the dorsal cervical region), but analysis of whorl direction and position was undertaken only for whorls present in >10% of dogs. This included assessment of whorls in the ventral mandibular, chest, brachial and thoracic axillary, elbow, and ischiatic regions. Where there was no variation in direction (e.g. in the case of brachial axillary and ischiatic whorls), or classification, these regions were not analysed.

The statistical package GenStat (10th edition, VSN International) was used in the analyses. Due to the differing logistics involved in conducting the three laterality tests, we evaluated the usefulness of each of these tests individually so that guide dog organisations could easily identify the potential usefulness of each. Therefore, each test was analysed separately and a combined model incorporating significant variables from the differing tests was not evaluated. A logistic generalised linear mixed model (GLMM) with 'group' as a random effect was used to assess the influence of the 'predictor variables' on the 'binary outcome variable', success in the GDTP.

Predictor variables (i.e. fixed effects) used in the GLMM included: (1) animal variables (age, breed, and sex); (2) motor laterality variables (direction, strength, paw preference category, and use of both paws); (3) sensory laterality variables (wither height, launching paw, jump success, approach distance, forepaw, hindpaw and lowest body part clearance heights, and the laterality indices for jump success, approach distance, forepaw, hindpaw and lowest body part clearance heights); and (4) whorl variables (presence, position, and direction).

Each term for the motor and structural laterality analyses were fitted in a separate model. All terms for the sensory lateralisation test were fitted in a single multivariable model. Each model also included terms for age, breed, sex, and group. Significance was determined at a level of $P \leqslant 0.05$, with values between 0.05 and 0.10 considered marginally non-significant and demonstrating only a tendency towards significance. The 'goodness-of-fit' of the logistic regression models was assessed in two ways. The adequacy of the linear variable (on the logit scale) was assessed by adding higher order polynomial terms (e.g. quadratic and cubic). However, in all cases higher-order terms were either non-significant, or inclusion of cubic terms, though significant, resulted in predicted models unreliable over the range of values. Hence, the linear-only models were fitted. Secondly, the overall fit of the model was assessed by the 'unweighted sum of squares' method (Hosmer et al., 1997) using the rsm library in R (R Development Core Team, 2010). Test statistics were non-significant indicating adequate model fit.

Results

Of the 114 dogs participating in this study, 50% successfully completed the GDTP. Of the animals that failed, 24.6% did so because of health reasons, and 75.4% because of behavioural problems. The results analysed were those relating to the dogs that were successful in training, or those that failed the training programme because of behavioural problems. Dog factors including 'sex' ($P = 0.97$), 'breed' ($P = 0.56$), 'age' ($P = 0.13$), and 'wither height' ($P = 0.48$), were not associated with the outcome in the training programme.

The full results of the motor, sensory, and structural lateralisation logistic regression analyses are detailed in Table 1. All three laterality tests were conducted and analysed independently of each other. Therefore, the inclusion of a dog in one laterality test did not bias the outcome of another test. Although several potentially significant findings were identified, some caution must be taken in their interpretation, as analysing large numbers of predictor variables may yield some false positive results.

Motor laterality: paw preference

The distribution of paw preferences based on the three categories (right-preferent, left-preferent, or ambidextrous), are listed in Table 2.

Direction

Success in training was significantly associated with the direction of laterality (median (m), −2.00; lower quartile (Q_1), −24.00;

Table 1
Details of the motor, sensory, and structural lateralisation regression analyses to determine associations between lateralisation tests in trainee guide dogs and success in the Guide Dog Training Programme. Motor (Kong test) and structural laterality analyses were based on 100 dogs, while the motor (First-stepping test) and sensory laterality analyses were based on 99 and 74 animals, respectively. Each term for the motor and structural laterality analyses were fitted in a separate model. All terms for the sensory lateralisation test were fitted in a single multivariable model. Each model also included terms for age, breed, sex, and group.

Term	Level	Odds ratio	95% Confidence interval	P[*]
Motor laterality – paw preference				
Kong LI[b]	(Covariate)	1.017	1.002, 1.032	0.028
First-stepping LI	(Covariate)	1.002	0.995, 1.010	0.542
Kong strength	(Covariate)	0.983	0.959, 1.007	0.167
First-stepping strength	(Covariate)	0.978	0.962, 0.994	0.007
Kong paw preference	Left vs. ambidextrous	0.281	0.090, 0.876	0.043
	Right vs. ambidextrous	1.091	0.311, 3.827	
First stepping paw preference	Left vs. ambidextrous	0.672	0.196, 2.302	0.745
	Right vs. ambidextrous	0.932	0.352, 2.469	
Kong – both paw uses	Yes vs. no	0.939	0.831, 1.060	0.303
First stepping – both paw uses	Yes vs. no	1.161	0.786, 1.715	0.446
Sensory laterality – ocular preference				
Wither height	(Covariate)	0.726	0.462, 1.142	0.164
Launching paw	Left vs. right	0.521	0.008, 36.165	0.760
Approach distance	(Covariate)	0.960	0.874, 1.056	0.398
Forepaw clearance height	(Covariate)	1.263	0.678, 2.350	0.457
Hindpaw clearance height	(Covariate)	1.750	1.232, 2.485	0.002
Lowest body part clearance height	(Covariate)	0.711	0.231, 2.190	0.547
Jump success	(Covariate)	1.547	0.508, 4.715	0.437
Approach distance LI	(Covariate)	1.292	0.965, 1.730	0.084
Forepaw clearance height LI	(Covariate)	1.152	1.027, 1.293	0.017
Hindpaw clearance height LI	(Covariate)	1.116	0.997, 1.249	0.055
Lowest body part clearance height LI	(Covariate)	0.957	0.823, 1.112	0.557
Jump success LI	(Covariate)	0.615	0.437, 0.865	0.006
Structural laterality – hair whorls				
Whorl presence				
Left cephalic whorl	Yes vs. no	0.693	0.038, 12.598	0.801
Right cephalic whorl	Yes vs. no	–[a]	–[a]	0.884
Left cervical whorl	Yes vs. no	–[a]	–[a]	0.884
Right cervical whorl	Yes vs. no	1.502	0.114, 19.723	0.752
Ventral mandibular whorl	Yes vs. no	0.734	0.211, 2.554	0.620
Chest whorl	Yes vs. no	0.516	0.085, 3.126	0.462
Left brachial axillary whorl	Yes vs. no	1.480	0.187, 11.727	0.705
Right brachial axillary whorl	Yes vs. no	1.515	0.083, 27.557	0.775
Left thoracic axillary whorl	Yes vs. no	1.350	0.335, 5.446	0.667
Right thoracic axillary whorl	Yes vs. no	1.194	0.398, 3.583	0.747
Left elbow whorl	Yes vs. no	1.047	0.247, 4.442	0.950
Right elbow whorl	Yes vs. no	1.047	0.247, 4.442	0.950
Left shoulder whorl	Yes vs. no	0.604	0.114, 3.208	0.546
Right shoulder whorl	Yes vs. no	0.204	0.019, 2.144	0.176
Left abdominal whorl	Yes vs. no	0.693	0.038, 12.598	0.801
Right abdominal whorl	Yes vs. no	–[a]	–[a]	0.884
Left ischiatic whorl	Yes vs. no	1.498	0.450, 4.981	0.501
Right ischiatic whorl	Yes vs. no	1.467	0.399, 5.398	0.556
Whorl position				
Chest whorl – % distance from TI[c]	(Covariate)	0.852	0.837, 0.868	0.077
Chest whorl – side of midline	Left vs. right	1.159	0.449, 2.992	0.756
Ventral mandibular whorl – % distance from TI	(Covariate)	1.095	0.812, 1.476	0.577
Ventral mandibular whorl – side of midline	Left vs. right	–[a]	–[a]	0.927
Left brachial axillary whorl – distance from midline	(Covariate)	0.646	0.240, 1.740	0.378
Right brachial axillary whorl – distance from midline	(Covariate)	0.982	0.296, 3.263	0.976
Left thoracic axillary whorl – % distance from TI	(Covariate)	1.088	0.808, 1.466	0.571
Left elbow whorl – distance from olecranon	(Covariate)	1.018	0.285, 3.636	0.977
Right elbow whorl – distance from olecranon	(Covariate)	1.211	0.288, 5.097	0.790
Left ischiatic whorl – distance from midline	(Covariate)	0.837	0.573, 1.221	0.345
Left ischiatic whorl – % distance from TI	(Covariate)	0.987	0.625, 1.560	0.955
Right ischiatic whorl – distance from midline	(Covariate)	0.768	0.535, 1.102	0.143
Right ischiatic whorl – % distance from TI	(Covariate)	1.075	0.709, 1.630	0.727
Whorl direction				
Ventral mandibular whorl	CC[d] vs. C[e]	–[a]	–[a]	0.941
Chest whorl	CC vs. C	0.254	0.063, 1.031	0.050
Left thoracic axillary whorl	CC vs. C	–[a]	–[a]	0.964
Right thoracic axillary whorl	CC vs. C	–[a]	–[a]	0.928
Left elbow whorl	CC vs. C	0.765	0.184, 3.179	0.707
Right elbow whorl	CC vs. C	7.085	0.715, 70.218	0.088

[*] P value for test of significance of term.
[a] Asymptotic standard errors were extremely large and therefore non-informative.
[b] LI, lateralisation index.
[c] TI, thoracic inlet.
[d] CC, counter-clockwise.
[e] C, clockwise.

Table 2
Distribution of dog paw preference based on the three paw categories: right-preferent, left-preferent, or ambidextrous, using the Kong ($n = 100$) and First-stepping ($n = 99$) tests.

Paw preference category	Kong test	First-stepping test
Right-preferent	24.0%, $n = 24$	48.5%, $n = 48$
Left-preferent	29.0%, $n = 29$	31.3%, $n = 31$
Ambidextrous	47.0%, $n = 47$	20.2%, $n = 20$

upper quartile (Q_3), 16.00) using the Kong test ($P = 0.028$). For each unit increase in laterality index, and hence shift to a right directional bias, the odds of an animal being successful increased by 1.7%. In the First-stepping test, the direction of laterality was not a significant predictor of success ($P = 0.54$).

Strength

Strength of laterality was significantly associated with the success of a dog in the GDTP as determined using the First-stepping (m, 52.00; Q_1, 28.00; Q_3, 72.00; $P = 0.007$), but not the Kong ($P = 0.17$) test. For each unit increase in lateral strength, the odds of success in the GDTP were reduced by a factor of 0.98.

Paw preference

The category of paw preference as determined using the First-stepping test was not associated with success in training ($P = 0.75$). However, a significant difference between paw preference categories as determined by the Kong test demonstrated that left-preferent animals had a lower success rate than right-preferent and ambidextrous dogs (left-preferent, 37.9%; right-preferent, 66.7%; ambidextrous, 63.8%; $P = 0.043$). The distribution of paw preferences as determined by the Kong test, and their relative pass rate are detailed in Table 3.

Both paws

Success in the GDTP was not associated with the number of 'both paw' uses by the dog in either the Kong ($P = 0.30$) or First-stepping ($P = 0.45$) tests.

Sensory laterality: ocular preference

Sensory Jump test measures

Clearance height of the hindpaw over the jump (m, 6.27; Q_1, 4.50; Q_3, 7.93), irrespective of ocular treatment, was associated with success in the GDTP ($P = 0.002$). Dogs had a 75.0% increase in the odds of success with each 1 cm increase in hindpaw clearance height. The distribution of hindpaw clearance heights and the predicted probabilities of success based on the logistic regression model are presented in Figs. 1 and 2, respectively. Forepaw and lowest body part clearance heights, wither height, and launching paw were not predictive of success ($P > 0.16$ in each case).

Success in the GDTP was also associated with a number of laterality indices based on the outcome of the SJT. The probability of success for these indices, as generated by the logistic regression model, is detailed in Fig. 3. The laterality index for clearance height of the forepaws (m, −0.85; Q_1, −5.81; Q_3, 2.25) was predictive of

Table 3
Success rate of dogs ($n = 100$) in the Guide Dog Training Programme based on paw preference categories (using the Kong test).

Paw preference category	Outcome of guide dog training		
	Total	Successful	Unsuccessful
Right-preferent	24.0%, $n = 24$	67.7%, $n = 16$	33.3%, $n = 8$
Left-preferent	29.0%, $n = 29$	37.9%, $n = 11$	62.1%, $n = 18$
Ambidextrous	47.0%, $n = 47$	63.8%, $n = 30$	36.2%, $n = 17$

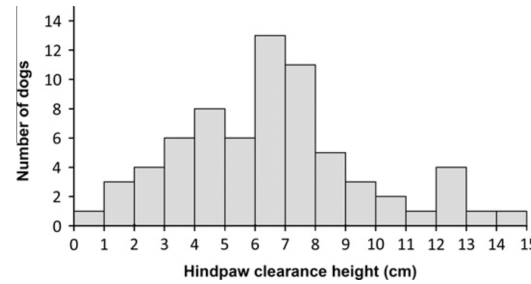

Fig. 1. Distribution of hindpaw clearance heights in a trainee guide dog population ($n = 74$) in the Sensory Jump test.

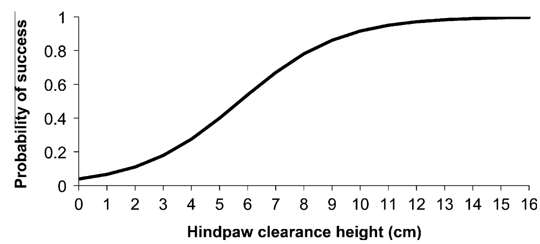

Fig. 2. Effect of hindpaw clearance height on the probability of success in the Guide Dog Training Programme.

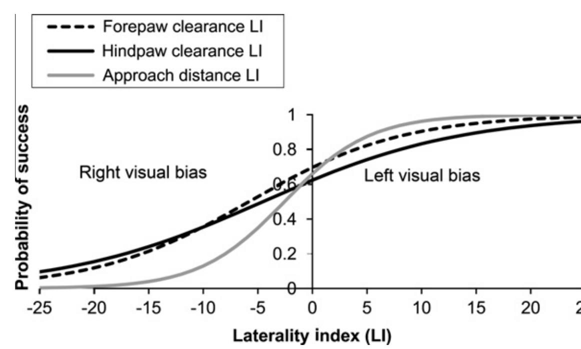

Fig. 3. Effect of Sensory Jump test laterality indices (LI) on the probability of success in the Guide Dog Training Programme, where positive and negative LIs represent left and right monocular vision bias, respectively.

success ($P = 0.017$), and clearance height of the hindpaws (m, −0.33; Q_1, −4.00; Q_3, 2.50) showed a tendency towards significance ($P = 0.055$). The odds of success increased by 15.2% and 11.6% for every unit increase in the laterality index (shift towards left monocular vision bias) for forepaw and hindpaw clearance heights, respectively. The approach distance LI (m, −0.87; Q_1, −2.18; Q_3, 1.09) was marginally non-significant ($P = 0.084$), where the odds of success in training increased by 29.3% for every LI unit increase, or shift towards left monocular vision bias.

Structural laterality: hair whorls

Presence

Whorls in the cephalic, cervical (dorsal, lateral, and ventral), thoracic and brachial axillary, chest, shoulder, elbow, abdominal, and ischiatic regions, were not associated with success in the GDTP ($P > 0.18$ in each case).

Position

Success in the GDTP was not associated with the position of ventral mandibular, brachial, thoracic axillary, elbow, or ischiatic whorls ($P > 0.14$ in each case). The side of the midline on which the chest whorl was located was not predictive of success ($P = 0.76$). However, the distance of a chest whorl from the thoracic inlet (m, 5.43; Q_1, 4.22; Q_3, 7.72) was marginally non-significant ($P = 0.077$). For every 1% increase in the distance away from the thoracic inlet, the odds of a dog being successful in training were reduced by 15%.

Direction

The direction of a chest whorl was significantly associated with success ($P = 0.050$). The success rate was 61% for dogs with a counter-clockwise chest whorl, whereas this was reduced to only 29% for animals with a clockwise chest whorl. Of the 91% of dogs that had a chest whorl present, 14% had a clockwise orientation (Fig. 4). A marginally non-significant relationship was noted between the direction of a right elbow whorl and success in the GDTP, in that dogs with a clockwise whorl at this location were more successful than animals with a counter-clockwise whorl (87.5% vs. 54.2%; $P = 0.088$). The direction of whorls located in other regions was not significantly associated with success ($P > 0.71$ in each case).

Discussion

Dogs play a variety of important roles in our society. In addition to their most common role as companions, they also perform a crucial function in guiding, police, security, customs, and military contexts. The convention to 'left-heel' train dogs, especially those in service, may result in erroneously judging dogs that are less behaviourally flexible to the right as non-compliant, for example, when executing rapid turns to the right. Such errors in judgment may result in otherwise valuable animals being rejected from training programmes. Given the significant resources, in terms of both time and money, spent training service dogs, it is worth exploring whether visual and limb biases affect the suitability of animals for work such as guiding.

This study investigated if motor, sensory, and structural measures of lateralisation could be used to predict the success or otherwise of dogs entering guide dog training. The success rate of 50% found in the current study is fairly typical of that achieved in other guide dog organisations (Ennik et al., 2006; Batt et al., 2008a), indicating that the population of dogs we assessed was representative of the general population of animals entering Guide Dog Training Programmes. Individual dog factors such as sex, breed, and age, were not associated with the training outcome. This finding was beneficial in that it allowed dogs to be treated equally when assessing laterality measures as predictors of success. Despite the traditional belief (Goddard and Beilharz, 1982) that female dogs are more successful in training, the lack of a sex difference reported in our study concurs with previous findings (Batt et al., 2008b).

Dogs entering the GDTP are generally 12–18 months of age. Not many studies have assessed age at commencement of training as a predictor of success. At this stage, although the majority of dogs have reached sexual maturity, most have not attained social maturity (Overall, 1997), and it remains unknown if this immaturity influences the animal's ability to learn. Our study suggests that age is not associated with a dog's ultimate ability to succeed in guide training. This information may provide guide dog organisations with a potential means of reducing puppy-raising costs, through assessing and training animals at an earlier age.

There are conflicting reports regarding the most suitable breed of dog to use in guiding. Although the present study did not find a breed effect, concurring with previous work (Goddard and Beilharz, 1983; Batt et al., 2008a), other studies reported breed differences with Labrador–Golden retriever crosses being the most, and German shepherds being the least, successful, respectively (Ennik et al., 2006). Although 114 dogs were assessed in the current study, given the vast majority (85%) were Labrador retrievers, a definitive breed effect could not be ascertained.

The direction of laterality and corresponding paw preference category were predictive of success in training. This finding supports our hypothesis that right-preferent animals were more successful; as dogs shifted from a left towards a right bias, their probability of success increased. An essential requirement of a guide dog is the ability to work with a visually impaired handler in a variety of environments, including challenging and novel situations. Given that a number of studies have reported fearfulness and withdrawal from novel situations as being associated with left-preferent animals (Hopkins and Bennett, 1994; Cameron and Rogers, 1999; Larose et al., 2006), it is perhaps unsurprising that the left-preferent dogs in our study were less successful than their right preferent counterparts. Studies have reported the stability over time of paw preference in the dog (Branson, 2006; Batt et al., 2008c), illustrating the reliability of this type of assessment tool in training programmes. Given the stability of this preference, additional benefits may be accrued if this test is applied to younger pups.

In comparison to the direction of motor laterality, success in the GDTP decreased as motor laterality strength increased. This finding was surprising, as previous reports indicated that dogs with a weaker paw preference were more reactive and took longer to recover from loud noises, as well as having longer latencies to drop and rest in a 'passive test' (Branson and Rogers, 2006; Batt et al., 2008b), which together would appear to be undesirable traits in guide dogs. It is possible that some behavioural characteristics associated with being strongly lateralised may run counter to the qualities needed for guide work. For example, if being strongly lateralised reduces behavioural flexibility, behaviourally rigid animals may struggle to over-ride trained responses autonomously (e.g. halting in traffic despite being cued by the handler to advance).

Batt et al. (2008b) also reported that success in guide training was high when the rate of both paws being used in the Kong test was low. Given the rate of both paw uses was determined post hoc in the study by Batt et al. (2008b), the current study measured both paw usage at the time of testing, and assessed a greater number of animals (114 vs. 43). The occurrence and number of both paw uses did not predict success. Dogs generally steadied the 'Kong' with one paw. However some dogs, on some occasions, recruited their second paw for this purpose. This action does not represent a shift towards ambidexterity (absence of a significant paw preference), but instead is a different measure, one which does not appear to predict success in guide training.

Identifying measures of motor laterality as predictors of success in the GDTP, may promote their application as additional tools for trainers when assessing potential guide dogs. By removing or reducing the number of left-preferent animals in training, a higher success rate would be anticipated (left-preferent, 37.9%;

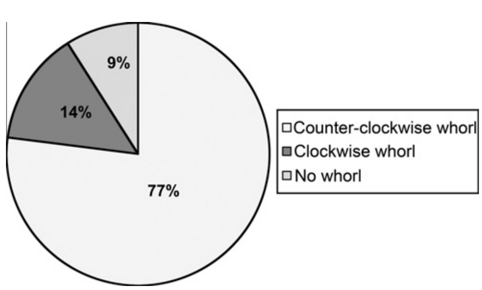

Fig. 4. Pie-chart illustrating the distribution and direction of chest hair whorls in trainee guide dogs ($n = 100$).

right-preferent, 66.7%; ambidextrous, 63.8%), along with the savings accrued from re-homing non-suitable animals at an earlier time-point.

Vertical clearance of the hindpaw in the SJT was strongly predictive of success in training. Since the wither height of the dog was not a significant predictor, the extra height clearance over the jump was not merely a product of the dog's physical stature, but probably a measure of more precise agility, which also resulted in these animals being more successful. Although dogs initially required concentration and focus to clear the jump with their forepaws, we hypothesise that sustained concentration and focus combined with a persistent spatial awareness during the jump permit greater hindpaw clearance heights.

It is possible that dogs that maintain accuracy and spatial awareness during jumping may be more focused during training. Both of these characteristics (spatial awareness and sustained concentration) are important traits for guide dogs, and this may explain why dogs with higher hindpaw clearances had a greater probability of success. Furthermore, the dogs with the lower clearance heights may have been manifesting fatigue or a lack of motivation for the task. Lack of motivation and predisposition to fatigue are undesirable traits in guide dogs, and may reflect attributes that contribute to a decreased likelihood of success in dogs with lower hindpaw clearance height.

While determining visual preference during jumping, we found that as dogs moved from a right to a left monocular bias for both fore and hindpaw clearance heights, they were more successful in training. This finding concurs with previous studies in other species which indicate analysing spatial information is typically perceived by the animal's left side, and hence processed by the right hemisphere (Cowell et al., 1997; Rogers, 2002). Given that when a guide dog is working, it continuously needs to analyse and process spatial information to assist its visually impaired handler through a variety of environments, this helps to explain why LMV preferent animals have a higher success rate than their RMV counterparts.

A number of sensory laterality measures can predict success in training. By adopting the SJT, guide dog organisations could identify left visually preferent dogs (i.e. with a higher probability of success), but also assess hindpaw clearance heights, regardless of visual preference. By adding a sensory test such as this to existing assessment protocols, success rates could be improved, and dogs less likely to succeed in training could be re-homed at an early stage.

The position and direction of the chest whorl were significant predictors of success in the GDTP. An increased probability of success was observed for dogs with counter-clockwise chest whorls, and when chest whorls were positioned closer to the thoracic inlet. The relationship between hair whorls and brain development can be attributed to the nervous system and integument sharing common ectodermal embryonic origins (Smith and Gong, 1974). Over the past few decades, research investigating hair whorl characteristics, including position and direction of cephalic whorls, have revealed associations with temperament in cattle (Grandin et al., 1995; Randle, 1998; Lanier et al., 2001) and horses (Barker, 1990; Murphy and Arkins, 2004, 2005; Górecka et al., 2006, 2007; Randle et al., 2011). An association between cephalic (scalp) whorl direction and behaviour has been described in humans where patients with schizophrenia have an increased frequency of counter-clockwise whorls (Alexander et al., 1992). Our study found that the direction of a chest hair whorl is predictive of success in the GDTP (an outcome largely based on behavioural tendencies), so it seems likely that a similar link between whorl direction and behavioural attributes occurs in dogs.

Cattle with a whorl positioned above the eyes are more reactive than those with whorls below the eye level. In the current study, a similar relationship is reported in relation to position of chest whorls; the more caudal the whorl, the lower the probability of success in the GDTP. Given success is largely based on the behavioural tendencies of the dog, this finding suggests that in dogs, an association between hair whorls and temperament does exist. This was an interesting finding and supports the findings of our previous study of this feature (Tomkins and McGreevy, 2010b). In our pilot study, the source of the dog (shelter vs. non-shelter) indicated a tendency towards being associated with the position of a chest whorl relative to the thoracic inlet, in that dogs from shelters had whorls further away from the inlet than non-shelter dogs (Tomkins and McGreevy, 2010b). Given that the predominant reason why owners relinquish their dogs to shelters are related to behaviour, including aggression (Salman et al., 2000), the finding of both our pilot and reported study suggest that chest whorl position may be an indicator of undesirable behavioural tendencies. However, it seems improbable that a single undesirable trait would underlie both the surrendering of dogs to shelters and the failure to complete guide dog training. To date, the present study is the first to investigate the relationship between whorls in regions other than the head, and apply this feature as an outcome based largely on behavioural tendencies.

Of all the measures of laterality provided in this study, the whorl, a structural marker of lateralisation, could potentially provide an early morphological indicator of success, as the integument develops in utero and is not influenced by nurture. Therefore, it may provide a valuable adjunct in guide dog assessment programmes. Although whorl position will vary between pups and sexually mature dogs due to differential growth of the integument, the direction of a hair whorl does not change, and could potentially be assessed on dogs as young as 8 weeks.

By only selecting dogs with counter-clockwise chest whorls, the probability of success could increase significantly as these dogs had a success rate twice that of dogs with clockwise whorls (61% vs. 29%), thereby reducing the cost of training a qualified guide dog. An example of how this measure of structural laterality could be used in conjunction with motor and sensory laterality tests to

Table 4
Success rate of dogs in the Guide Dog Training Programme based on the categorisation of structural (hair whorl) and motor (paw preference) laterality measures. Success rate is based on 91 dogs that had both a chest whorl present and that participated in the Kong test.

Chest whorl direction	Paw preference category	Success rate in training (%)
Counter-clockwise, $n = 77$	Ambidextrous, $n = 39$	64.1
	Right, $n = 18$	72.2
	Left, $n = 20$	45.0
Clockwise, $n = 14$	Ambidextrous, $n = 4$	50.0
	Right, $n = 3$	33.3
	Left, $n = 7$	14.3

Table 5
Success rate of dogs in the Guide Dog Training Programme based on the categorisation of structural (hair whorl) and sensory (hindpaw clearance height) laterality measures. Success rate is based on 60 dogs that had both a chest whorl present and that participated in the Sensory Jump test. A threshold of $\leqslant 5$ cm was used to categorise hindpaw clearance heights, as dogs with lower clearance heights had a <50% probability of success.

Chest whorl direction	Hindpaw clearance height	Success rate in training (%)
Counter-clockwise, $n = 55$	>5 cm, $n = 36$	72.2
	$\leqslant 5$ cm, $n = 19$	57.9
Clockwise, $n = 5$	>5 cm, $n = 4$	25.0
	$\leqslant 5$ cm, $n = 1$	0.0

aid guide dog trainers in identifying dogs with a higher success rate in training is illustrated in Tables 4 and 5, respectively. If the three laterality tests are used in combination, selection of dogs with a counter-clockwise chest whorl, that were right-preferent, and that had a hindpaw clearance height >5 cm, would result in the selection of 10% of the total young dog population. Our findings predict that these animals would have a success rate of 83.3% in guide dog training.

Conclusions

To our knowledge, this is the first study to report that all three measures of laterality, motor, sensory, and structural, can be used to predict the suitability of dogs for guiding work. Measures of lateralisation associated with increased likelihood of success in guide dog training included: (1) direction and categorisation of motor laterality where right-preferent dogs were more successful; (2) STJ measures of hindpaw clearance height, and a shift towards left monocular bias for forepaw and hindpaw clearance heights and approach distance; and (3) chest whorls that were counter-clockwise in direction, and were positioned closer to the thoracic inlet. Identification of early predictors of success in training may increase the efficiency with which suitable dogs are selected, and target the allocation of expensive training resources to the most suitable animals. However, given that association and causation are not synonymous, it is possible that our findings could have arisen by chance or through some other unmeasured variable. Therefore, we recommend that guide dog organisations exercise some caution before applying the findings of this study.

Conflict of interest statement

None of the authors of this paper has a financial or personal relationship with other people or organisations that could inappropriately influence or bias the content of the paper.

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