Journal of Comparative Psychology
2016, Vol. 130, No. 4, 313–320

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0735-7036/16/$12.00 http://dx.doi.org/10.1037/com0000030

Lateral Bias and Temperament in the Domestic Cat (*Felis silvestris*)

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Research points to a relationship between lateralization and emotional functioning in humans and many species of animal. The present study explored the association between paw preferences and emotional functioning, specifically temperament, in a species thus far overlooked in this area, the domestic cat. Thirty left-pawed, 30 right-pawed, and 30 ambilateral pet cats were recruited following an assessment of their paw preferences using a food-reaching challenge. The animals' temperament was subsequently assessed using the Feline Temperament Profile (FTP). Cats' owners also completed a purpose-designed cat temperament (CAT) scale. Analysis revealed a significant relationship between lateral bias and FTP and CAT scale scores. Ambilateral cats had lower positive (FTP+) scores, and were perceived as less affectionate, obedient, friendly, and more aggressive, than left or right-pawed animals. Left and right pawed cats differed significantly on 1 trait on the CAT scale, namely playfulness. The strength of the cats' paw preferences was related to the animals' FTP and CAT scores. Cats with a greater strength of paw preference had higher FTP + scores than those with a weaker strength of paw preference. Animals with stronger paw preferences were perceived as more confident, affectionate, active, and friendly than those with weaker paw preferences. Results suggest that motor laterality in the cat is strongly related to temperament and that the presence or absence of lateralization has greater implications for the expression of emotion in this species than the direction of the lateralized bias.

Keywords: cats, emotion, handedness, paw preferences, temperament

Lateralized motor behavior has been studied as an observable measure of cerebral functional asymmetry for numerous years (e.g., Harris, 1983; Springer & Deutsch, 1989). The most prominent manifestation of lateralized behavior in humans is that of handedness (i.e., the predominant use of one hand), with roughly 90% of people using their right hand for most activities (Annett, 1985; Porac & Coren, 1981).

The preferred use of one hand is associated with greater activity of the contralateral hemisphere (Yousry et al., 1995). The two hemispheres differ significantly in their functions, including emotional processing, although there is still debate as to the exact contribution of each hemisphere in this role (for reviews see Davidson, 1995; Demaree, Everhart, Youngstrom, & Harrison, 2005). The right hemisphere is generally considered to be responsible for the processing of fearful information, encouraging withdrawal from novel stimuli and situations (e.g., Ahern & Schwartz, 1979). The left hemisphere, by contrast, largely inhibits fear, encouraging exploration and approach behavior (e.g., Silberman & Weingartner, 1986). Dominance, or more frequent use, of one hemisphere over the other predisposes individuals to behave in a certain way. Left-handed or weakly lateralized individuals are more likely to be fearful and prone to maladaptive behavior than right-handed or strongly lateralized individuals (e.g., Rogers, 2010). For example, people who are strongly lateralized (i.e., demonstrate a dominant right or left hand preference for specific activities) are significantly less prone to anxiety disorders than individuals who are ambilateral (Watson, Clark, & Tellegen, 1988). People with weak hand preferences are also more likely than those with strong hand preferences to suffer from posttraumatic stress disorder (e.g., Farina et al., 2012), schizophrenia (e.g., Hirnstein & Hugdahl, 2014), and psychosis (Barrantes-Vidal et al., 2013).

Until recently, it was assumed that lateralized behavior was unique to humans. Studies of motor bias in other species (e.g., amphibians, rodents, cats, primates, marsupials, whales), however, suggest that cerebral functional asymmetry may be a fundamental feature of all vertebrate, and even some invertebrate, brains (for reviews see Frasnelli, Vallortigara, & Rogers, 2012; MacNeilage, Rogers, & Vallortigara, 2009; Rogers, 2002; Rogers, Vallortigara, & Andrew, 2013; Vallortigara, Chiandetti, & Sovrano, 2011; Vallortigara & Rogers, 2005). Like humans, many species of animal also demonstrate a relationship between limb preference and emotional functioning (for reviews see Leliveld, Langbein, & Puppe, 2013; Versace & Vallortigara, 2015). Left-hand dominant chimpanzees (*Pan troglodytes*), for example, interact with novel stimuli less willingly than right-handed individuals (Hopkins & Bennett, 1994). Gordon and Rogers (2015) found that left-handed marmosets (*Callithrix jacchus*) were more likely than right-handed animals to exhibit a negative cognitive bias, while nonlateralized chicks (*Gallus gallus domesticus*) have been shown to exhibit more distress calls in response to the sight of a predator than their more strongly lateralized counterparts (Dharmaretnam & Rogers, 2005).

This article was published Online First June 30, 2016.

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We thank all of the cats and owners who participated in this study. Louise J. McDowell was funded by a DEL studentship.

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Although less extensively studied, a relationship between motor bias and emotional functioning has also been observed in quadrupeds, notably the dog, *Canis familiaris*. Branson and Rogers (2006), for example, found that dogs with noise sensitivity were more likely to be ambilateral than strongly left- or right-paw preferent. Batt, Batt, Baguley, and McGreevy (2008) found that the direction and strength of paw preference in prospective guide dogs determined the animals' suitability for a working role, with more strongly lateralized animals displaying more confidant and relaxed behavior (e.g., in a social contact test with an unfamiliar person), than those with weaker paw preferences. The same authors (Batt, Batt, Baguley, & McGreevy, 2009) found that dogs with stronger paw preferences showed reduced latencies to catch a moving object, arguing that this reflected a bolder disposition. In a similar vein, Tomkins, Thomson, and McGreevy (2010) reported that right-preferent dogs were more likely to successfully complete a Guide Dog training program, and that the probability of success increased as animals shifted from a left-toward a right-paw preference bias.

The domestic cat, *Felis silvestris*, is another quadrupedal species that has been shown to exhibit lateral motor behavior in the form of paw preferences (e.g., Pike & Maitland, 1997; Wells & Millsopp, 2009), with relative stability in motor bias by 1 year of age (Wells & Millsopp, 2012). To date, the relationship between lateralization and emotional functioning in the cat has been subject to no investigation. The following study therefore aimed to explore the association between paw preferences in the domestic cat and one expression of emotional functioning, namely feline temperament. Temperament, or personality, has attracted considerable attention in nonhuman animals (for review see David & Dall, 2016), more recently the felids (e.g., Gartner, Powell, & Weiss, 2014; Gartner & Weiss, 2013). Although studies have varied considerably in terms of their assessment methods (e.g., surveys, behavioral assessments) and dimensions of personality investigated, most are consistent in acknowledging that cats have personality traits which can be measured reliably (Gartner & Weiss, 2013). These traits can be related to numerous outcome measures, for example, health and well-being, response to captivity, and so forth (e.g., Deary, Weiss, & Batty, 2010). Whether they are related to motor asymmetry is still unknown, although given the link in other species (see earlier), one might expect an association.

For the purpose of this study, 90 cats were assessed for their paw preferences using a complex food-reaching challenge. The animals' temperament was subsequently determined using the Feline Temperament Profile (Siegford, Walshaw, Brunner, & Zanella, 2003). Owners were also required to complete a purpose-designed cat temperament (CAT) scale as an additional measure of feline personality. It was hoped that the study would provide pioneering information on the relationship between motor bias and emotional functioning in a species that has thus far been overlooked in this area and advance understanding on the potential advantages and functions of cerebral asymmetry.

Method

Subjects

Domestic pet cats were recruited via response to an email advertising a study on feline paw preferences sent to cat breeders and pet owners in Northern Ireland, United Kingdom. An equal number of left, right, and ambilateral cats was sought for inclusion in the sample. One hundred and seven cats of mixed breed were initially recruited and tested for their paw preferences. From this, 90 cats (46 male, 44 female) were randomly chosen and used in the final dataset. Thirty of the cats were classified as left-pawed, 30 as right-pawed, and the remainder as ambilateral. Animals ranged from 1 to 17 years of age (mean age = 3.14 +/– SEM 0.31 years). All of the cats were family pets living in households, and whose owners had consented to them taking part in the study. None of the cats had undergone any behavioral training, nor had any disability preventing them from completing the study.

Paw Preference Test

The Catit Senses Food Maze (Catit, United Kingdom) was used to test the cats' paw preferences. This is a 35.6-cm tall spherical feeding "tower," comprising 3 levels into which food can be placed. The food is accessed via 3 holes on each level (see Figure 1). Similar food reaching tasks have been used successfully to assess motor bias in the cat (e.g., Pike & Maitland, 1997; Wells & Millsopp, 2009, 2012). For the purpose of this study, the top level of the food maze was removed as it proved too high for the cats to put their paws into without standing on their rear legs and compromising balance.

Prior to the start of the first trial, the cat was shown, and allowed to sniff, the food treat (Dreamies, Mars Petcare, United Kingdom—small squares of cheese flavored cat treats). As the cat watched, 10 treats were placed on the top (i.e., second) level of the food maze. Since the food could be accessed through 3 holes, it was ensured that the cat was placed directly in front of 1 hole for each trial. As and when required (i.e., once all the food treats had been accessed by the cat), another 10 treats were placed in the food maze. A single trial comprised the cat placing its paw inside the food maze and attempting to remove the treat. Only once the paw had been removed from the maze did the next trial begin. The paw the cat used to attempt food retrieval, regardless of whether or not a treat was retrieved, was recorded. Each cat was tested until 50 responses were made. No reward, be it tactile (comforting, strok-



Figure 1. Subject using the Catit Senses Food Maze.

ing) or social (verbal praise or smiling), was provided during the task.

Feline Temperament Profile

The Feline Temperament Profile (FTP; Siegford et al., 2003) was used to assess the cats' temperament. The FTP is a standardized test, based on a model proposed by Lee and colleagues (1983). The test is designed to measure a cat's emotional reactions to a series of interactions with an unfamiliar person. It was developed originally to determine the suitability of cats to be used as therapy animals by evaluating general levels of aggressiveness, sociability, and adaptability. The test comprises 10 phases during which an unfamiliar person (the experimenter) carries out a series of interactions with the cat, ranging from calling the animal's name through to picking the cat up and stroking it (see Table 1 for full details). A number of behavioral responses are recorded for each phase of the test, some considered to be "acceptable" (FTP+), others as "questionable" (FTP–; see Table 1). For example, during Phase 1 (initial approach), the behavior of "makes eye contact with the Experimenter" is deemed an acceptable response. If this behavior is displayed by the subject, a score of 1 is recorded for FTP+; if the behavior is absent, it receives a score of 0. Similarly, the behavioral response "retreats/adopts defensive position" (Phase 1) is treated as a "questionable" reaction, and, if observed, a score of 1 is recorded for FTP–. The occurrence (+1) or absence (0) of each of the listed responses is summed, generating an overall FTP+ score and an overall FTP-score, each measuring two aspects of feline temperament. The test has been shown to be stable over time and to correlate well with ethological observations of cats' interactions with people (Siegford et al., 2003).

Prior to testing, the FTP was carried out on 10 healthy pet cats (not included as subject animals for this investigation). Interob-

Table 1
The Feline Temperament Profile (FTP) Procedure and Scoring System (E Refers to Experimenter) Adapted From Iki, Ahrens, Pasche, Bartels, & Erhard, 2011

Phase of test	Sequence of events	Scoring	
		Acceptable responses (FTP+)	Questionable responses (FTP–)
Phase 1 initial approach	E kneels down 6 feet from cat and calls the animal several times with one hand extended.	Makes eye contact with E Vocalizes Approaches E Rolls over Sniffs E's hand	Avoids eye contact with E Retreats/adopts defensive position Looks at E but does not approach
Phase 2 follow-up approach	E moves closer to cat (3 feet) if it does not respond to the initial approach and calls the animal's name again	Makes eye contact with E Vocalizes Approaches E Rolls over Sniffs E's hand	Avoids eye contact with E Retreats/adopts defensive position Looks at E but does not approach Arches back and/or hisses
Phase 3 friendliness	E holds out hand to cat such that it is lower than the animal's head.	Sniffs E's hand Licks/rubs body against E's hand Rubs head against E's hand Rolls over Vocalizes	Retreats/adopts defensive position Strikes/threatens to strike E's hand Bites/attempts to bite E's hand
Phase 4 interaction	E strokes cat on head, sides, and back, while talking to the animal. Test terminates at this point if cat refuses to allow an interaction.	Rubs against E's legs or hand Purrs, meow, or chirrups Bumps head against E Circles around E Shows initial fear but then relaxes	Defensive/threatening posture Strikes/threatens to strike E's hand Bites/attempts to bite E's hand Withdraws from E
Phase 5 play initiation	E moves backwards from cat and pulls a piece of string along floor to encourage play.	Approaches E for more stroking Watches the string Chases the string	Ignores the string Does not look at E
Phase 6 sociability 1	E calls cat by its name and waits for it to approach. Failing this, E approaches cat, strokes it, and attempts to pick it up and cradle it against his/her chest.	Appears relaxed Makes eye contact with E Extends paw towards E	Attempts to escape Strikes/threatens to strike E Bites/attempts to bite E
Phase 7 sociability II	E strokes cat while on his/her lap.	Purrs/rubs against E's hand Makes eye contact with E Rolls over Stands up to smell E's face and/or places paws on neck	Sits on E's lap reluctantly Jumps off E's lap Threatens or becomes aggressive, e.g., bites or scratches
Phase 8 adaptability	Cat is placed on the floor and E calls to the animal, while motioning with his/her hands.	Jumps onto E Makes eye contact with E but remains on floor Stands on hind legs against E	Ignores E Moves away from E
Phase 9 aggressiveness/fear 1	E pulls cat's tail firmly while the animal is on the floor.	Rolls over Shows no reaction Tries to escape or struggle	Strikes/threatens to strike E Growls/hisses
Phase 10 aggressiveness/fear II	E drops metal object behind cat while it is on the floor and not looking.	Startles but quickly relaxes Shows no reaction	Startles, then runs to hide Startles, then shows a defensive/aggressive posture Does not appear to hear the noise

server reliability was determined to be 90% for the FTP+ and 94% for the FTP– scores, respectively. The cat's paw preferences were tested as outlined earlier 10 min following the end of the FTP.

Cat Affect and Temperament Scale

A purpose-designed questionnaire, referred to as the Cat Affect and Temperament (CAT) scale, adapted from Serpell (1996), was developed to assess owners' perceptions of their cats' temperament. The scale comprises 12 traits (playful, confident, affectionate, excitable, obedient, active, friendly, intelligent, quiet, clean, independent, aggressive). Owners are required to indicate how strongly they believe each trait describes their cat on a 5-point Likert scale, ranging from 1 (*very weakly*) to 5 (*very strongly*).

Procedure

Cats and their owners were tested individually in their own homes. Testing commenced with the FTP to prevent familiarization with the experimenter (LM). Each animal underwent the test outlined above, moving sequentially from Phase 1 through to Phase 10. The experimenter conducted the test, while another individual observed the cat and recorded their reactions (FTP+ and FTP–) as per Siegford and colleagues (2003). Each cat's owner was present throughout testing, although did not interact with its pet at any point. The data collection for the task was conducted over the course of roughly 1 hr per cat. Owners completed the CAT scale while their pet was having its paw preferences tested.

Data Analysis

Fifty paw responses per animal were recorded during the paw preference test. Binomial *z* scores were calculated to determine whether the frequency of right- or left-paw use exceeded that expected by chance. An alpha value of 0.05 was adopted for all analyses. A *z* score greater than +1.96 (two-tailed) reflected a significant left paw preference, while a *z* score less than −1.96 indicated a significant right paw preference. Cats with *z* scores between +1.96 and −1.96 were classified as ambilateral. A directional handedness index (HI) was calculated (see Wells, 2003) to quantify each cat's paw preference on a continuum from strongly left-paw preferent (+1) to strongly right paw-preferent (−1). The HI was calculated by dividing the difference between the total number of left and right paw reaches by their sum (L – R)/(L + R). The strength of the cats' paw preferences was calculated by taking the absolute value of each HI score (ABS-HI).

Two-way analyses of variance (ANOVAs) were carried out to determine whether there was a relationship between feline sex (male, female), the direction of the cats' paw preferences (left, right, ambilateral), and the animals' FTP+ and FTP– scores.

Principal component analysis with direct oblimin rotation was used to identify significant relationships between the 12 items on the CAT scale. The number of components extracted was determined by a scree plot. Items that straddled components were assigned to the factor with the highest loading. One-way ANOVAs were conducted to examine the relationship between the direction of the subjects' paw preferences (left, right, ambilateral) and each of the factors arising from the principal component analysis. Further ANOVAs examined the relationship between the direction of cats' paw preferences and each of the 12 owner-rated traits (e.g., playful, confident, etc.) on the CAT scale.

Pearson moment correlations were conducted to determine whether there was a relationship between FTP+ and FTP– scores and to examine the relationship between the strength of the cats' paw preferences (ABS-HI) and their FTP+ and FTP– scores. Further correlations were carried out to examine the relationship between the strength of the cats' paw preferences and individual CAT scale traits.

Ethical Note

All methods adhered to the Association for the Study of Animal Behavior/Animal Behavior Society Guidelines for the Use of Animals in Research (Association for the Study of Animal Behaviour, 2006). Ethical approval for the study was granted by the Research Ethics Committee, School of Psychology, QUB.

Results

FTP

A significant negative correlation was unearthed between the FTP+ and FTP– scores, $r(90) = -0.93$, $p < .001$. This strong negative correlation points to a lack of discrimination between the FTP+ and FTP–; both scales appear to be measuring the same latent construct. For this reason, subsequent analysis was only carried out using the data from the FTP+ scores.

There was a significant relationship between the cats' paw preferences and their FTP+ scores, $F(2, 84) = 544.89$, $\eta^2 = 0.66$, $p < .001$. Post hoc tests showed that cats classified as ambilateral had significantly ($p < .001$, Bonferroni test) lower FTP+ scores ($M = 3.18$, ±95% CI 2.06–4.29) than animals classified as left- ($M = 10.98$, ±95% CI 9.60–12.36) or right- ($M = 11.06$, ±95% CI 9.85–12.26) pawed. Feline sex was not significantly related to the animals' FTP scores, $F(1, 84) = 13.28$, $\eta^2 = 0.02$, $p = .23$.

CAT Scores

Principal component analysis and examination of the scree plot revealed two factors, each accounting for 25% of the variance. Based on both the loadings and previous factor analysis of domestic cat personality traits (Gartner et al., 2014), these components were labeled "neuroticism" and "impulsiveness." Table 2 presents the factor structures of mean trait ratings. Loadings <= 0.4 are suppressed. One-way ANOVAs on the two factors revealed a significant relationship between the cats' paw preferences and the factor of neuroticism, $F(2, 87) = 14.38$, $\eta^2 = 0.25$, $p < .001$. Pairwise comparisons showed that ambilateral cats had significantly higher mean scores for this factor ($M = -0.69$, ±95% CI −1.01–0.37) than left- ($M = 0.25$, ±95% CI −0.07–0.57) or right- ($M = 0.44$, ±95% CI 0.12–0.76) pawed animals. There was no significant relationship between feline paw preferences and the factor of impulsiveness, $F(2, 87) = 0.91$, $\eta^2 = 0.02$, $p = .41$.

Analysis of the 12 scale items on the CAT revealed a significant relationship between the animals' paw preferences and owners' perceptions of their pets' temperament for 5 of the 12 characteristics examined (see Table 3). Post hoc *t* tests showed that cats with

Table 2
Factor Structures of Mean Trait Ratings From the CAT Scale (1 = Very Low Likelihood of Displaying Trait; 5 = Very High Likelihood of Displaying Trait)

Item	Neuroticism	Impulsiveness
Playful		−.78
Confident	.65	
Affectionate	.62	
Excitable		.77
Obedient	.67	
Active		−.81
Friendly	.74	
Intelligent	.54	
Quiet		−.65
Clean	.54	
Independent		.47
Aggressive	−.54	

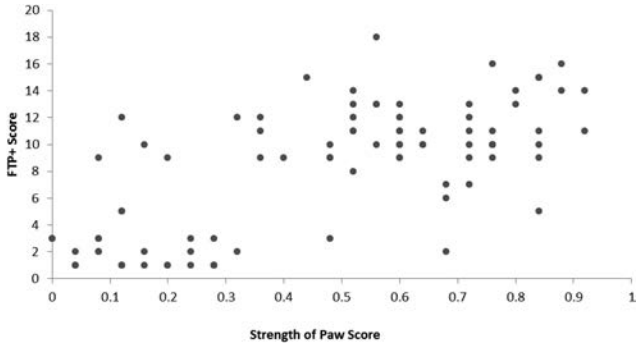


Figure 2. Scattergraph showing the correlation between the cats' strength of paw scores and their FTP+ scores.

a right paw preference were rated as significantly ($p < .05$) more playful than left-pawed or ambilateral cats. Ambilateral cats were also perceived to be significantly ($p < .05$) less affectionate, obedient, friendly, and more aggressive than their left- or right-pawed counterparts.

Strength of Paw Preference and Feline Temperament

A significant positive correlation was discovered between the cats' strength of paw preference and their FTP+ score, $r(90) = 0.70$, $p < .001$ (see Figure 2). Strength of paw preference was significantly related to some of the owner-rated traits on the CAT scale (see Table 4). Stronger paw preferences were positively correlated with confidence, affection, activity, and friendliness scores. By contrast, there was a significant negative correlation between strength of paw preference and feline aggression.

Discussion

The findings from the present study suggest that motor laterality in the domestic cat is strongly related to feline temperament. The results demonstrate that cats classified as ambilateral on a food-reaching challenge respond in a more fearful manner on a temperament test, and are perceived by their owners to harbor different personality traits, than animals classified as left- or right-paw preferent. The results from the investigation revealed virtually no difference in the temperament of left- or right-pawed cats and suggest that strength of lateralization is more important for emotional functioning in this species than the direction of the lateral bias.

The cats' paw preferences in this study were found to be very significantly related to both the positive and questionable scores on the Feline Temperament Profile (FTP) and owners' perceptions of their pets' personality as assessed by the CAT scale. Animals classified as ambilateral had significantly lower FTP + scores and were rated by their owners as more aggressive and less affectionate, obedient, and friendly, than cats with a left/right paw preference. Following a factor analysis, ambilateral cats were found to have higher mean scores for components labeled "neuroticism" than left- or right-pawed animals. No significant differences emerged in either the FTP or CAT scores of the left- and right-pawed cats, apart from owners' perceptions of the animals' playfulness, which were found to be higher in right-than left-pawed animals. Previous studies have pointed to a relationship between ambilaterality and fearful responses to aversive stimuli; individu-

Table 3
Mean (±95% CI) Owner Perceptions Scores on the CAT Scale (1 = Very Low Likelihood of Displaying Trait; 5 = Very High Likelihood of Displaying Trait) and ANOVA Results

	Paw preference			
Trait	Left	Right	Ambilateral	ANOVA
Playful	3.93 (3.53–4.34)	4.33 (3.93–4.74)	3.53 (3.13–3.94)	$F(2, 87) = 3.87$, $\eta^2 = .08$, $p = .02$
Confident	3.97 (3.51–4.42)	4.00 (3.54–4.46)	3.30 (2.84–3.76)	$F(2, 87) = 2.96$, $\eta^2 = .06$, $p = .06$
Affectionate	4.20 (3.82–4.57)	4.30 (3.92–4.67)	3.27 (2.89–3.64)	$F(2, 87) = 9.12$, $\eta^2 = .17$, $p < .001$
Excitable	2.93 (2.43–3.44)	2.43 (1.93–2.94)	2.80 (2.29–3.31)	$F(2, 87) = 1.03$, $\eta^2 = .02$, $p = .36$
Obedient	3.70 (3.27–4.12)	3.70 (3.27–4.12)	2.97 (2.54–3.39)	$F(2, 87) = 3.91$, $\eta^2 = .08$, $p = .02$
Active	3.53 (3.07–3.99)	4.00 (3.54–4.46)	3.23 (2.77–3.69)	$F(2, 87) = 2.77$, $\eta^2 = .06$, $p = .07$
Friendly	4.43 (4.04–4.82)	4.53 (4.14–4.92)	3.17 (2.78–3.56)	$F(2, 87) = 14.00$, $\eta^2 = .26$, $p < .001$
Intelligent	4.17 (3.81–4.52)	4.13 (3.77–4.49)	3.97 (3.61–4.32)	$F(2, 87) = .35$, $\eta^2 = .01$, $p = .70$
Quiet	3.03 (2.59–3.47)	2.33 (1.89–2.77)	2.57 (2.12–3.01)	$F(2, 87) = 2.57$, $\eta^2 = .06$, $p = .08$
Clean	4.60 (4.32–4.88)	4.67 (4.38–4.95)	4.47 (4.18–4.75)	$F(2, 87) = .51$, $\eta^2 = .01$, $p = .60$
Independent	3.60 (3.11–4.09)	3.87 (3.37–4.36)	3.17 (2.67–3.66)	$F(2, 87) = 2.02$, $\eta^2 = .04$, $p = .14$
Aggressive	1.10 (.83–1.37)	1.10 (.83–1.37)	2.20 (1.93–2.47)	$F(2, 87) = 21.84$, $\eta^2 = .33$, $p < .001$

Table 4
Correlation of Owner-Rated Feline Traits and Strength of Paw Preference Scores

Trait	R	P
Playful	.17	.10
Confident	.24	.02
Affectionate	.33	.001
Excitable	−.06	.56
Obedient	.20	.06
Active	.22	.03
Friendly	.44	<.001
Intelligent	.05	.63
Quiet	.05	.61
Clean	.03	.78
Independent	.16	.14
Aggressive	−.49	<.001

als with a more strongly dominant hemisphere appear to be better able to deal with stress than those who do not rely on one hemisphere over the other (Rogers, 2010). For example, Branson and Rogers (2006) found that ambilateral dogs were more reactive to the sound of fireworks than animals classified as left-or right-paw preferent. Ambilateral chicks have been shown to emit more distress calls in response to the sight of a predator than their more lateralized counterparts (Dharmaretnam & Rogers, 2005), while, in humans, posttraumatic stress disorder and alexithymia have been linked to mixed-handedness (Parker, Keightley, Smith, & Taylor, 1999; Spivak, Segal, Mester, & Weizman, 1998; Zeitlin, Lane, O'Leary, & Schrift, 1989). Interestingly, Schneider, Delfabbro, and Burns (2013) found no significant relationship between paw preference and canine temperament, as assessed by an owner-based temperament scale, the Canine Behavioral Assessment and Research Questionnaire (CBARQ; Duffy & Serpell, 2012). The authors concluded that the personality scale may not be a sensitive enough tool to detect differences between individuals based on their lateral bias and recommended assessing temperament with more objective measures of behavior. The present study, however, utilized two approaches in the measurement of cat temperament and found that owner-based ratings of their pets' behavior were largely comparable with the behavioral assessment of feline temperament. Work is currently underway to explore lateral bias and temperament in the domestic dog using two methodological approaches to the assessment of canine personality.

The strength of the cats' paw preferences in this study was also related to the animals' FTP and CAT scores. Cats with a greater strength of paw preference had higher FTP+ scores than those with a weaker strength of paw preference. In a similar vein, analysis revealed significant positive correlations between strength of "pawedness" and owners' ratings of certain feline traits. These results are in line with those of Batt and colleagues (2009) who reported more relaxed and confident behaviors in potential guide dogs with a stronger paw preference compared with more weakly lateralized animals, and, taken in conjunction with the results reported above, further suggest that weakly lateralized cats, like other species, may be more vulnerable to stress than those which rely more heavily on one hemisphere over the other.

It is interesting to note that the ambilateral cats in this study were perceived by their owners as more aggressive than animals classified as left- or right-pawed. Aggression is processed in the right hemisphere in many species. For example, Anolis lizards show a preference for using their left eye during aggressive interactions (Deckel, 1995), while domestic dogs have been shown to turn their heads more toward threatening stimuli (silhouettes of snakes and threatening cats) that are presented on their left-hand side as opposed to their right-hand side (Siniscalchi, Sasso, Pepe, Vallortigara, & Quaranta, 2010), wag their tails more to the left-hand side when presented with visual stimuli (e.g., unfamiliar person) that might be expected to elicit withdrawal tendencies (Quaranta, Siniscalchi, & Vallortigara, 2007) and even appear sensitive to directional tail wagging in conspecifics (Siniscalchi, Lusito, Vallortigara, & Quaranta, 2013). Physical aggression has also been found to be correlated with weak lateralization in male psychiatric patients (Hillbrand, Sokol, Waite, & Foster, 1993). Although further work is needed to support this, the results from the present investigation provide preliminary evidence to suggest that aggression in the cat, as in other species, may have its basis in lateralization.

Several authors have reported an association between direction of motor bias and emotional functioning, with left-limbed animals showing stronger fear responses than those with a right-sided bias. Left-handed marmosets (Cameron & Rogers, 1999) and chimpanzees (Hopkins & Bennett, 1994), for instance, are less likely than right-handed individuals to approach and interact with novel objects. Gordon and Rogers (2015) likewise found that left-handed marmosets were more likely than right-handed animals to exhibit a negative cognitive bias. Interestingly, no significant differences in FTP scores emerged between the left- and right-pawed cats in this study. Further work is needed to explore this and determine whether this is a generic trait in cats or a function of the experimental design adopted in this investigation, although the former seems more likely in light of the fact that two methodological approaches were used here. It may also be worthwhile in future studies exploring for the role of other individual factors that may exert an effect on both feline personality and motor bias, for example, castration status, rearing background, littermate effects, and so forth.

One of the limitations of this study is the reliance on pet cats as subjects, which, it could be argued, may show a certain degree of homogeneity in terms of temperament. Indeed, this no doubt explains the strong negative correlation between the FTP+ and FTP– scores unearthed in the study. The subjects are presumably meeting the criteria required to be a pet cat, namely, they are high on "acceptable" temperament traits and low on "questionable" ones. Future studies of this kind may benefit from recruiting cats from other sources (e.g., rescue shelters) in an effort to increase breadth of personality difference. This study also failed to explore for breed differences. Research has shown a relationship between lateral bias and breed, a trait related to personality, in horses (McGreevy & Thomson, 2006), although not in dogs (McGreevy, Brueckner, Thomson, & Branson, 2010). Whether there is an association between breed and motor asymmetry in cats is unknown and would be worthy of study.

It has been suggested that lateralization may offer survival advantages (Vallortigara & Rogers, 2005). A lateralized brain is better able to facilitate a shift of focus from a negative, potentially aversive stimulus, to a less intimidating one (Rogers, Zucca, & Vallortigara, 2004). Branson and Rogers (2006) hypothesized that

nonlateralization of neural functions may be related to stronger emotional response to stimulation. The results from the present study lend support for this and suggest that in the cat, a previously overlooked species in this area, the presence or absence of lateralization has greater implications for the expression of emotion than the direction of the lateralized bias. Whether this is a fundamental feature that can be found at any level of phylogeny remains unknown, but there is certainly evidence in its favor.

References

Ahern, G. L., & Schwartz, G. E. (1979). Differential lateralization for positive versus negative emotion. *Neuropsychologia, 17,* 693–698. http://dx.doi.org/10.1016/0028-3932(79)90045-9

Annett, M. (1985). *Left, right, hand and brain: The right shift theory*. New York, NY: Erlbaum.

Association for the Study of Animal Behaviour. (2006). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour, 71,* 245–253. http://dx.doi.org/10.1016/j.anbehav.2005.10.001

Barrantes-Vidal, N., Gross, G. M., Sheinbaum, T., Mitjavila, M., Ballespí, S., & Kwapil, T. R. (2013). Positive and negative schizotypy are associated with prodromal and schizophrenia-spectrum symptoms. *Schizophrenia Research, 145,* 50–55. http://dx.doi.org/10.1016/j.schres.2013.01.007

Batt, L. S., Batt, M. S., Baguley, J. A., & McGreevy, P. D. (2008). Factors associated with success in guide dog training. *Journal of Veterinary Behavior: Clinical Applications and Research, 3,* 143–151. http://dx.doi.org/10.1016/j.jveb.2008.04.003

Batt, L. S., Batt, M. S., Baguley, J. A., & McGreevy, P. D. (2009). The relationships between motor lateralization, salivary cortisol concentrations and behavior in dogs. *Journal of Veterinary Behavior: Clinical Applications and Research, 4,* 216–222. http://dx.doi.org/10.1016/j.jveb.2009.02.001

Branson, N. J., & Rogers, L. J. (2006). Relationship between paw preference strength and noise phobia in Canis familiaris. *Journal of Comparative Psychology, 120,* 176–183. http://dx.doi.org/10.1037/0735-7036.120.3.176

Cameron, R., & Rogers, L. J. (1999). Hand preference of the common marmoset (*Callithrix jacchus*): Problem solving and responses in a novel setting. *Journal of Comparative Psychology, 113,* 149–157. http://dx.doi.org/10.1037/0735-7036.113.2.149

David, M., & Dall, S. R. X. (2016). Unravelling the philosophies underlying "animal personality" studies: A brief re-appraisal of the field. *Ethology, 122,* 1–9. http://dx.doi.org/10.1111/eth.12445

Davidson, R. J. (1995). Cerebral asymmetry, emotion, and affective style. In R. J. Davidson & K. Hugdahl (Eds.), *Brain asymmetry* (pp. 361–387). Cambridge, MA: MIT Press.

Deary, I. J., Weiss, A., & Batty, G. D. (2010). Intelligence and personality as predictors of illness and death: How researchers in differential psychology and chronic disease epidemiology are collaborating to understand and address health inequalities. *Psychological Science in the Public Interest, 11,* 53–79. http://dx.doi.org/10.1177/1529100610387081

Deckel, A. W. (1995). Laterality of aggressive responses in Anolis. *The Journal of Experimental Zoology, 272,* 194–200. http://dx.doi.org/10.1002/jez.1402720304

Demaree, H. A., Everhart, D. E., Youngstrom, E. A., & Harrison, D. W. (2005). Brain lateralization of emotional processing: Historical roots and a future incorporating "dominance." *Behavioral and Cognitive Neuroscience Reviews, 4,* 3–20. http://dx.doi.org/10.1177/1534582305276837

Dharmaretnam, M., & Rogers, L. J. (2005). Hemispheric specialization and dual processing in strongly versus weakly lateralized chicks. *Behavioural Brain Research, 162,* 62–70. http://dx.doi.org/10.1016/j.bbr.2005.03.012

Duffy, D. L., & Serpell, J. A. (2012). Predictive validity of a method for evaluating temperament in young guide and service dogs. *Applied Animal Behaviour Science, 138,* 99–109. http://dx.doi.org/10.1016/j.applanim.2012.02.011

Farina, B., Mazzotti, E., Farina, F., Della Marca, G., Savoja, V., Kotzalidis, G. D., . . . Tatarelli, R. (2012). Relationship between handedness and persistent emotional distress in adults experiencing an earthquake. *Rivista di Psichiatria, 47,* 309–312.

Frasnelli, E., Vallortigara, G., & Rogers, L. J. (2012). Left-right asymmetries of behaviour and nervous system in invertebrates. *Neuroscience and Biobehavioral Reviews, 36,* 1273–1291. http://dx.doi.org/10.1016/j.neubiorev.2012.02.006

Gartner, M. C., Powell, D. M., & Weiss, A. (2014). Personality structure in the domestic cat (*Felis silvestris catus*), Scottish wildcat (*Felis silvestris grampia*), clouded leopard (*Neofelis nebulosa*), snow leopard (*Panthera uncia*), and African lion (*Panthera leo*): A comparative study. *Journal of Comparative Psychology, 128,* 414–426. http://dx.doi.org/10.1037/a0037104

Gartner, M. C., & Weiss, A. (2013). Personality in felids: A review. *Applied Animal Behaviour Science, 144,* 1–13. http://dx.doi.org/10.1016/j.applanim.2012.11.010

Gordon, D. J., & Rogers, L. J. (2015). Cognitive bias, hand preference and welfare of common marmosets. *Behavioural Brain Research, 287,* 100–108. http://dx.doi.org/10.1016/j.bbr.2015.03.037

Harris, L. J. (1983). Laterality of function in the infant: Historical and contemporary trends in theory and research. In G. Young, S. J. Segalowitz, C. M. Corter, & S. E. Trehub (Eds.), *Manual specialization and the developing brain* (pp. 177–247). New York, NY: Academic Press.

Hillbrand, M., Sokol, S. J., Waite, B. M., & Foster, H. G., Jr. (1993). Abnormal lateralization in finger tapping and overt aggressive behavior. *Progress in Neuro-Psychopharmacology & Biological Psychiatry, 17,* 393–406. http://dx.doi.org/10.1016/0278-5846(93)90073-2

Hirnstein, M., & Hugdahl, K. (2014). Excess of non-right-handedness in schizophrenia: Meta-analysis of gender effects and potential biases in handedness assessment. *The British Journal of Psychiatry, 205,* 260–267. http://dx.doi.org/10.1192/bjp.bp.113.137349

Hopkins, W. D., & Bennett, A. J. (1994). Handedness and approach-avoidance behavior in chimpanzees (Pan). *Journal of Experimental Psychology: Animal Behavior Processes, 20,* 413–418. http://dx.doi.org/10.1037/0097-7403.20.4.413

Iki, T., Ahrens, F., Pasche, K. H., Bartels, A., & Erhard, M. H. (2011). Relationships between scores of the Feline Temperament Profile and behavioural and adrenocortical responses to a mild stressor in cats. *Applied Animal Behaviour Science, 132,* 71–80. http://dx.doi.org/10.1016/j.applanim.2011.03.008

Lee, R. L., Zeglan, M. E., Ryan, T., & Hines, L. M. (1983). Guidelines: animals in nursing homes. *California Veterinarian, 3,* 22a–26a.

Leliveld, L. M. C., Langbein, J., & Puppe, B. (2013). The emergence of emotional lateralization: Evidence in non-human vertebrates and implications for farm animals. *Applied Animal Behaviour Science, 145,* 1–14. http://dx.doi.org/10.1016/j.applanim.2013.02.002

MacNeilage, P. F., Rogers, L. J., & Vallortigara, G. (2009). Origins of the left & right brain. *Scientific American, 301,* 60–67. http://dx.doi.org/10.1038/scientificamerican0709-60

McGreevy, P. D., Brueckner, A., Thomson, P. C., & Branson, N. J. (2010). Motor laterality in 4 breeds of dogs. *Journal of Veterinary Behavior: Clinical Applications and Research, 5,* 318–323. http://dx.doi.org/10.1016/j.jveb.2010.05.001

McGreevy, P. D., & Thomson, P. C. (2006). Differences in motor laterality in breeds of performance horse. *Applied Animal Behaviour Science, 99,* 183–190. http://dx.doi.org/10.1016/j.applanim.2005.09.010

Parker, J. D., Keightley, M. L., Smith, C. T., & Taylor, G. J. (1999). Interhemispheric transfer deficit in alexithymia: An experimental study. *Psychosomatic Medicine, 61,* 464–468. http://dx.doi.org/10.1097/00006842-199907000-00010

Pike, A. V. L., & Maitland, D. P. (1997). Paw preferences in cats (*Felis silvestris catus*) living in a household environment. *Behavioural Processes, 39,* 241–247. http://dx.doi.org/10.1016/S0376-6357(96)00758-9

Porac, C., & Coren, S. (1981). *Lateral preferences and human behavior*. New York, NY: Springer-Verlag. http://dx.doi.org/10.1007/978-1-4613-8139-6

Quaranta, A., Siniscalchi, M., & Vallortigara, G. (2007). Asymmetric tail-wagging responses by dogs to different emotive stimuli. *Current Biology, 17,* R199–R201. http://dx.doi.org/10.1016/j.cub.2007.02.008

Rogers, L. J. (2002). Lateralization in vertebrates: Its early evolution, general pattern, and development. *Advances in the Study of Behavior, 31,* 107–161. http://dx.doi.org/10.1016/S0065-3454(02)80007-9

Rogers, L. J. (2010). Relevance of brain and behavioural lateralization to animal welfare. *Applied Animal Behaviour Science, 127,* 1–11. http://dx.doi.org/10.1016/j.applanim.2010.06.008

Rogers, L. J., Vallortigara, G., & Andrew, R. J. (2013). *Divided brains: The biology and behaviour of brain asymmetries*. Cambridge, UK: Cambridge University Press. http://dx.doi.org/10.1017/CBO9780511793899

Rogers, L. J., Zucca, P., & Vallortigara, G. (2004). Advantages of having a lateralized brain. *Proceedings of the Royal Society of London, Series B: Biological Science, 271,* 420–422. http://dx.doi.org/10.1098/rsbl.2004.0200

Schneider, L. A., Delfabbro, P. H., & Burns, N. R. (2013). Temperament and lateralization in the domestic dog (*Canis familaris*). *Journal of Veterinary Behavior: Clinical Applications and Research, 8,* 124–134. http://dx.doi.org/10.1016/j.jveb.2012.06.004

Serpell, J. A. (1996). Evidence for an association between pet behavior and owner attachment levels. *Applied Animal Behaviour Science, 47,* 49–60. http://dx.doi.org/10.1016/0168-1591(95)01010-6

Siegford, J. M., Walshaw, S. O., Brunner, P., & Zanella, A. J. (2003). Validation of a temperament test for domestic cats. *Anthrozoös, 16,* 332–351. http://dx.doi.org/10.2752/089279303786991982

Silberman, E. K., & Weingartner, H. (1986). Hemispheric lateralization of functions related to emotion. *Brain and Cognition, 5,* 322–353. http://dx.doi.org/10.1016/0278-2626(86)90035-7

Siniscalchi, M., Lusito, R., Vallortigara, G., & Quaranta, A. (2013). Seeing left- or right-asymmetric tail wagging produces different emotional responses in dogs. *Current Biology, 23,* 2279–2282. http://dx.doi.org/10.1016/j.cub.2013.09.027

Siniscalchi, M., Sasso, R., Pepe, A. M., Vallortigara, G., & Quaranta, A. (2010). Dogs turn left to emotional stimuli. *Behavioural Brain Research, 208,* 516–521. http://dx.doi.org/10.1016/j.bbr.2009.12.042

Spivak, B., Segal, M., Mester, R., & Weizman, A. (1998). Lateral preference in post-traumatic stress disorder. *Psychological Medicine, 28,* 229–232. http://dx.doi.org/10.1017/S0033291797005837

Springer, S. P., & Deutsch, G. (1989). *Left brain, right brain*. New York, NY: Freeman.

Tomkins, L. M., Thomson, P. C., & McGreevy, P. D. (2010). First-stepping test as a measure of motor laterality in dogs (*Canis familaris*). *Journal of Veterinary Behavior: Clinical Applications and Research, 5,* 247–255. http://dx.doi.org/10.1016/j.jveb.2010.03.001

Vallortigara, G., Chiandetti, C., & Sovrano, V. A. (2011). Brain asymmetry (animal). *Wiley Interdisciplinary Reviews: Cognitive Science, 2,* 146–157.

Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralization. *Behavioral and Brain Sciences, 28,* 575–589. http://dx.doi.org/10.1017/S0140525X05000105

Versace, E., & Vallortigara, G. (2015). Forelimb preferences in human beings and other species: Multiple models for testing hypotheses on lateralization. *Frontiers in Psychology, 6,* 233. http://dx.doi.org/10.3389/fpsyg.2015.00233

Watson, D., Clark, L. A., & Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: The PANAS scales. *Journal of Personality and Social Psychology, 54,* 1063–1070. http://dx.doi.org/10.1037/0022-3514.54.6.1063

Wells, D. L. (2003). Lateralised behaviour in the domestic dog, *Canis familaris. Behavioural Processes, 61,* 27–35.

Wells, D. L., & Millsopp, S. (2009). Lateralised behaviour in the domestic cat, Felis silvestris catus. *Animal Behaviour, 78,* 537–541. http://dx.doi.org/10.1016/j.anbehav.2009.06.010

Wells, D. L., & Millsopp, S. (2012). The ontogeny of lateralised behaviour in the domestic cat, Felis silvestris catus. *Journal of Comparative Psychology, 126,* 23–30. http://dx.doi.org/10.1037/a0026522

Yousry, T. A., Schmid, U. D., Jassoy, A. G., Schmidt, D., Eisner, W. E., Reulen, H. J., . . . Lissner, J. (1995). Topography of the cortical motor hand area: Prospective study with functional MR imaging and direct motor mapping at surgery. *Radiology, 195,* 23–29. http://dx.doi.org/10.1148/radiology.195.1.7892475

Zeitlin, S. B., Lane, R. D., O'Leary, D. S., & Schrift, M. J. (1989). Interhemispheric transfer deficit and alexithymia. *The American Journal of Psychiatry, 146,* 1434–1439. http://dx.doi.org/10.1176/ajp.146.11.1434

Received November 11, 2015
Revision received February 29, 2016
Accepted March 1, 2016 ■