



Research report

The relationship between problem-solving ability and laterality in cats

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ABSTRACT

The association between hemispheric asymmetries and cognitive ability is one of the key areas of comparative laterality research. In several animal species, individual limb preferences correlate with perceptual, cognitive, or motor abilities, possibly by increasing dexterity of one limb and minimizing response conflicts between hemispheres. Despite this wealth of research, the association between laterality and cognitive abilities in the cat (*Felis catus*) is not well understood. Therefore, it was the aim of the present study to investigate the relationship between laterality and problem-solving ability in cats. To this end, strength and direction of paw preferences in 41 cats were measured using two novel food reaching tasks in which the animals needed to open a lid in order to reach the food reward. We found that cats that showed a clear preference for one paw were able to open more lids successfully than ambilateral animals. Moreover, cats that preferred to interact with the test apparatus with their paw from the beginning, opened more lids than cats the first tried to interact with the test apparatus using their heads. Results also suggested a predictive validity of the first paw usage for general paw usage. It was also shown that the cats' individual paw preferences were stable and task-independent. These results yield further support to the idea that lateralization may enhance cognitive abilities.

1. Introduction

Cerebral asymmetries are defined as morphological and functional differences between the two hemispheres of the brain [1]. Functional cerebral asymmetry (FCA) is thus defined as a specialization of one hemisphere to control certain cognitive functions to a greater extent than the other hemisphere [2]. This is reflected in lateralized behaviour, such as handedness – the most apparent functional expression of cerebral asymmetry in humans [1]. In the vast majority of humans, one hand is clearly more dominant than the other for fine motor activities such as writing and drawing. In about 90% of the human population, the dominant hand is the right hand [3,4].

Initially, it was assumed that cerebral asymmetries were unique for humans and that they might be a characteristic feature of our species. Consequently, several studies assumed that this difference resulted from a genetic mutation which occurred after hominins diverged from apes [5–7]. However, recent studies demonstrate that hemispheric

asymmetries are a major principle of brain organization in many vertebrates [8,9] and invertebrates [10]. As a result of a systematic study on the limb preferences of 119 non-human vertebrate species, it was found that only 38 (31.93%) of the investigated species showed neither individual nor population-level asymmetry [8].

If lateralization is so widespread, it should provide an evolutionary advantage. This could reflect a reduction of cognitive response selection time by minimizing neural conflict between hemispheres [11]. According to Rogers [12], lateralized brains can process diverse information from different sources in parallel in both hemispheres. Thus, lateralized individuals would be expected to have higher perceptual, cognitive, and motor abilities. This hypothesis was supported by studies in many species such as chimpanzees [13], pigeons [14], chicks [15] and parrots [16]. For example, in a study comparing a cognitively demanding multitasking ability of lateralized and non-lateralized chicks, lateralized chicks were found to be more likely to be alert to possible predators and to simultaneously find food [15]. Similar results were

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obtained by Piddington and Rogers [17] who concluded that strength of hand preference is related to higher ability to detect predators and perform foraging simultaneously in marmosets. Another study investigating the success of pigeons on grain-grit discrimination has suggested that increased visual asymmetry enhances success by increasing the cognitive ability in pigeons [14].

Paw preference [18] and head-orienting response to auditory stimuli [19] have been used as the main indicators of functional lateralization in cats. The first studies on paw preferences were conducted by Graystyan and Molnar in 1954 by using a food reaching task to determine paw preferences of cats [20,21]. They discovered that out of 15 cats, 8 were right-pawed, 4 left-pawed, and 3 ambilateral. A year later, contrary to Graystyan and Molnar, Cole [22] reported that the number of left-pawed cats was higher than that of right-pawed cats. Interestingly, ambilaterality had a higher frequency than both left-pawedness and right-pawedness in this study. The number of conflicting results further increased with subsequent studies. While some of the authors suggested that cats have a rightward bias [23,24], other authors suggested that cats have a leftward bias at the population level [25,26]. A recent meta-analysis study on paw preference of cats and dogs finally reported that cats do not show a population level asymmetry. However, 78% of cats showed individual level asymmetry to the left or the right [27]. The authors proposed that these varied findings could result from small sample sizes and different paw preference assessment methodologies such as food reaching, toy reaching or reaching for moving targets. These diverging results have led to the need to develop a standard paw preference determination test.

Although cats live with humans for thousands of years [28] and are one of the most socialized species towards humans [29], they are considered semi-domesticated due to their low levels of behavioural, morphological, and genomic differences to wildcats [30]. Moreover, many cat populations are not isolated from wild ancestors, and their food and reproduction cycles are still independent from humans [31]. Very likely, the majority of cat populations are less affected by the Domestication Syndrome (DS) than other domesticated species. DS is often characterized by major changes in morphological and behavioural characteristics [32]. For instance, the grey wolf (*Canis lupus*) is the closest living relative of domestic dogs and these species diverged from the same ancestor 36,900–41,500 years ago [33]. In one study, pet dogs were found to be less successful in problem-solving in comparison to free-ranging domestic dogs and human socialized wolf [34] and this finding suggested that cognitive ability of domestic dogs was significantly affected by domestication, beside the distinct changes in morphological characteristics. It was proposed that DS has negative effects upon problem-solving behaviour by affecting cognitive ability due to the alteration and modifications in Neural Crest Cell (NCC) migration [32]. Since brain tissues originate from the neural plate that is formed by NCCs [35], domestication syndrome could have an important impact on functional cerebral asymmetries.

Although a large number of species show a wide diversity of cognitive capabilities [36], the majority of animal cognition studies focused on large-brained mammals, such as primates [37] and cetaceans (dolphins and whales) [38], thereby neglecting smaller-brained mammals like cats. Especially, the link between cognitive abilities and laterality is not well understood in this species. Therefore, it was the main aim of the present study to evaluate this link.

Animal studies on innovative skills and problem-solving discovered a positive correlation between problem-solving ability and general learning capacity [39–41]. Here we hypothesized that the strength of lateralized behaviour, as expressed in strength of paw preference, is positively correlated with the ability of problem-solving in cats. The studies on common marmosets demonstrated that hand preferences are stable across different reaching tasks [42,43]. Considering the similar manipulative abilities of primates and cats while reaching for food, we further hypothesized that paw preferences of cats are consistent across different food-reaching tasks. To our knowledge, this study is the first

that aims to understand the relationship between paw preferences and problem-solving ability in cats.

2. Experimental procedures

2.1. Subjects

Subjects of this study consisted of 41 healthy domestic cats (22 males [13 spayed], 19 females [10 neutered]), of various breeds, aged between 6 months and 14 years old. The sterilization status of 3 cats was unknown. All of the cats were family pets and informed consents were obtained from the cats' owners prior to the study. Ethical approval for this study was obtained from the Animal Experiments Local Ethics Committee, Ankara University (2018-17-108).

2.2. Experimental setup

The testing protocol was conducted in cat hotels, which are specialized facilities providing routine care and accommodation to cats when owners have to leave them temporary. Each cat was tested individually in the area (cage/room) where it spent most of its time. Standard enrichment materials, such as litterbox, food and water bowls, were positioned separately in the cage environment. All of the cats were provided with private resting areas and enough free space to walk around in their cages. Although sizes of the cages were not standard, the minimum floor space provided for each cat was 1.5 m² and minimum height was 2 m. Nothing was removed from the cage before or during the test in order not to cause any stress for the cats. The problem-solving tests included two steps (T1, T2) which had different designs. All tests were performed by the same two experimenters. Each cat was tested by one of the experimenters. During the testing procedure, the observer sat centrally in front of the cage to observe the paw usage of cats. She sat at the possible farthest position from the cats in order not to distract the cats. The testing apparatus was placed at the center of the testing environment. Both tests were presented in front of the cats and were parallelly positioned to the front of the cage.

2.2.1. Test 1

For the first problem-solving test, four mini transparent capless sauce cups (3 cm high, 4 cm dia) were attached on a wooden block (35 cm × 20 cm × 1 cm) upside down. Canned food was placed under the cups, so that the cups served as lids for the food. Cats could smell the food out through the holes in the cups. All lids could be opened towards the same direction, and the test device was given in the same direction to all cats (Fig. 1). The lids were opening in the opposite direction to the cat's position so that the opening is facing the cat. The experiment started with test 1, which was considered to be easier than test 2.

2.2.2. Test 2

Unlike the first problem-solving test, the second test had a different design, including different types of lids (0.5 cm high, 4 cm diameter), each of which opened towards different directions (Fig. 2). In contrast to the first test, the food rewards were not placed directly on the wooden surface of the test apparatus, but inside the cup. Thus, the animals had to reach inside the cup after opening the lids in the second test. Therefore, the second test is likely more complex than the first test and potentially requires more paw movements in order to be solved correctly.

Many paw movements were required to open the lids to reach the food in both tests. Total count of the paws used in the test was measured to determine the strength and direction of the laterality.

2.3. Procedure

None of the cats received any training before or during the study. There were no food restrictions for the cats during the study. Tests were



Fig. 1. A cat performing the first problem solving test: The cat should open the lids towards the correct direction to reach the food.

performed at any time of the day when the cats were thought to be motivated to eat the canned food that was used as a reward. Before each session, the experimenter was introduced to the tested cats in order to observe the social interaction between the cat and the experimenter. During this introductory step, a small piece of wet food was offered to the cat by the experimenter. Accordingly, only the cats with a good social interaction and positive emotional states were included in the study. Although positions of the cats could not be standardized, the tests were initiated only when the cat paid attention to the experimenter and made eye contact with her. Cats did not receive any form of

positive reinforcement other than the food reward obtained in the test, such as social (*e.g.* verbal praise) or tactile (*e.g.* petting) interactions during testing. The testing apparatus was presented to cats only once in order to avoid any learning effect on paw preferences. The test was performed until the cat opened all of the cups or lost its interest in the tasks. The total number of interactions between the cats' paws and the test apparatus was recorded. The experimenter gave a small piece of wet food as a treat to cats at the beginning and end of each step in order to motivate the cat to the test and also to avoid frustration arising from incomplete play and/or hunting behaviour. The second problem-



Fig. 2. A cat performing the second problem-solving test. Cats had to first open the lids and then needed to reach inside the cups in order to gain access to the food reward. Each opening faced towards a different direction than the others.

solving test was presented to the cats immediately after the first problem-solving test was completed.

2.4. Behavioural analysis

The behaviour of the cats was video-recorded continuously during test sessions using a mobile phone camera positioned on a tripod located in front of the testing apparatus. Each time the cat touched the test apparatus in order to open the lids or reach for food was considered as a paw use. The experimenter recorded the paw that was first used by the cat trying to retrieve the food placed under the cups. The number of paw responses of the cats in the process of solving the tests was evaluated. The video footage was subsequently analyzed blindly by two trained observers, and interobserver reliability was assessed. The percentage of their agreement was always higher than 90%.

For each test, cats were considered successful when having opened one of the four sauce cups. To determine success degree of the cats, the number of the lids opened by the cat, and the reaction time of the cat was evaluated. The reaction time was defined as the time the animal needed in order to open all 4 lids for each test or until it lost interest in the tasks. Paw and head preference of the cats were also evaluated throughout the tests. To classify the cats as paw- or head-preferred, the first interaction with the test apparatus was analyzed. If an animal used a paw in this first interaction, it was classified as paw-preferent. If an animal used its head in this first interaction, it was classified as head-preferent. This classification was conducted for each cat separately for each test. The descriptions of behavioural parameters used in the analysis is given in Table 1.

In test 2 the acts of opening the lids and reaching for food require different motor skills. Here again, the number of paw response for reaching for food and the number of paw response for lid opening was also counted in order to evaluate these actions separately.

2.5. Statistical analysis

For all statistical tests, SPSS 21 was used. The strength of the paw preferences of the cats was determined using a Laterality index (LI), calculated using the formula $LI = (R - L)/(R + L)$. Here, R indicates the overall number of interactions with the test apparatus that were conducted with the right paw and L indicates the overall number of interactions with the test apparatus that were conducted with the left paw. The LI has a range between -1.0 (exclusive use of the left paw) and $+1.0$ (exclusive use of the right paw). In addition to LI's, we also calculated absolute LI's as an indicator of individual lateralization strength independently of the direction of the preference.

The significance of paw preference on the individual level was determined using binomial Z-scores for each cat [$z = (R - 0.5 N)/(0.25 N)$]. According to the equation, N refers to the total number of interactions with the test apparatus while R indicates the number of interactions in which the right paw is used. Cats with a positive Z-score value ($z \geq 1.96$) were scored as R-pawed, whereas those with a

negative Z-score value ($z \leq -1.96$) were scored as L-pawed. The other cats were determined as ambilateral (A).

We first assessed population level and individual level asymmetries, as well as the stability of individual preferences. In order to test paw preferences on the population level, one-sample *t*-tests with the average LI as the dependent variable were used. In order to test paw preferences on the individual level, the absolute LI was determined for each animal. We then used one-sample *t*- to test whether the average absolute LI differed from 0 to determine whether or not individual asymmetries existed in the present sample. Chi-Square tests were used to determine whether or not the distribution of left preferent, right-preferent and ambilateral cats was equal or not. LI's were also compared between subjects that used the left or the right paw first using independent sample *t*-tests. In order to assess whether one of the tasks was more complex, we compared average reaction time, and total number of paw uses to solve the task between task 1 and task 2 using dependent samples *t*-tests. We also assessed the relationship between lateralization and problem-solving ability. Total paw use, opened lids and reaction time were compared between lateralized and ambilateral subjects using independent samples *t*-test. Moreover, we observed during testing that some cats tried to solve the task using their mouths or heads first before they actually started using their paws. We therefore also compared conducted an exploratory analysis in which we compared problem-solving ability between head and paw preferent subjects using independent samples *t*-tests.

As several papers have suggested sex differences in cats paw preferences [18,27], we also assessed whether there were any sex effects on lateralization or problem-solving abilities in our sample. To this end, lateralization and problem-solving abilities were compared between male and female animals using independent samples *t*-tests. Moreover, lateralization and problem-solving abilities were compared between sterilized and non-sterilized animals using independent samples *t*-tests. Correlations were generally determined using Neyman-Pearson correlation coefficients. In general, effects were considered significant if the *p*-value was lower than 0.05.

3. Results

3.1. Population level and individual level asymmetries

3.1.1. Test 1

The average LI in test 1 was -0.08 . It was not significant at the population level ($t_{(37)} = -0.97$; $p = 0.34$). On the individual level, 10 animals showed a rightward preference, 12 a leftward preference, 16 were ambilateral, and for 3 no LI could be calculated, since they did not show a single paw movement in the task. This distribution also showed no population level asymmetry in this task ($\chi^2 = 1.47$; $p = 0.48$).

In order to statistically test whether individual level asymmetries existed in this task, we determined the absolute LI. Here it was shown that cats had an average absolute LI of $0.396 (+/-0.316)$ which was significantly different from 0 ($t_{(37)} = 7.73$; $p < 0.001$). Thus, cats showed individual level asymmetries in this task.

3.1.2. Test 2

In test 2, the average LI was -0.12 (SD = 0.43) overall, -0.06 (SD = 0.72) for food reaching and -0.04 (SD = 0.44) for lid opening. The LI failed to reach significance when compared to 0 for all three conditions (all *p*'s > 0.09), indicating that there again was no population level asymmetry in this task. This was also confirmed by the Chi-Square analyses of the numbers of right preferent, left preferent and ambilateral animals. Here, no deviation from equal distribution of the three categories was detected for any of the three dependent variables (all *p*'s > 0.49). The absolute LI's, however, were significantly different from zero for the overall test ($0.35 +/- 0.27$; $t_{(39)} = 8.25$; $p < 0.001$), for lid opening ($0.35 +/- 0.27$; $t_{(39)} = 8.19$; $p < 0.001$) and for food reaching ($0.61 +/- 0.36$; $t_{(31)} = 9.78$; $p < 0.001$). Thus, cats showed

Table 1

Detailed descriptions of the behavioural parameters.

Behavioural parameters	Description
Reaction time	Total time the animal spent in each test
Success	The animal was considered "successful" if one of the four sauce cups was opened by the cat
Success degree	Two parameters were considered: Number of the lids opened by the cat Reaction time of the cat
Paw-preferred	Animals using a paw in the first interaction with the test
Head-preferred	Animals using head in the first interaction with the test
Paw use	Touching the test apparatus by stretching foreleg to open the lids or reach for the food

Table 2

Individual paw preferences in cats for two tests [Sex: (F: female; M: male); Pref: paw preference (R: right paw; L: left paw; N: the overall number of paw uses per animal; A: ambilateral); LI: laterality index; Z-score: positive Z score values ($Z \geq 1.96$) indicate right lateral bias; negative Z-score values ($Z \leq -1.96$) indicate left lateral bias; -: value not calculated due to absence of paw intervention].

Cat	Sex	Test 1					Pref
		R	L	N	LI	Z- score	
1	F	5	32	37	-0.73	-4.44	L
2	M	0	0	0	-	-	-
3	F	45	91	136	-0.34	-3.94	L
4	F	16	36	52	-0.38	-2.77	L
5	F	49	62	111	-0.12	-1.23	A
6	M	0	15	15	-1.00	-3.87	L
7	F	9	21	30	-0.40	-2.19	L
8	F	35	37	72	-0.03	-0.24	A
9	F	20	27	47	-0.15	-1.02	A
10	M	64	46	110	0.16	1.72	A
11	F	90	1	91	0.98	9.33	R
12	M	0	3	3	-1.00	-1.73	A
13	F	40	17	57	0.40	3.05	R
14	F	13	8	21	0.24	1.09	A
15	M	17	23	40	-0.15	-0.95	A
16	M	0	0	0	-	-	-
17	F	0	0	0	-	-	-
18	M	27	7	34	0.59	3.43	R
19	F	4	18	22	-0.64	-2.98	L
20	M	24	10	34	0.41	2.40	R
21	F	72	67	139	0.04	0.42	A
22	M	24	62	86	-0.44	-2.22	L
23	M	24	44	68	-0.29	-2.43	L
24	M	21	19	40	0.05	0.32	A
25	F	53	33	86	0.23	2.16	R
26	F	0	10	10	-1.00	-3.16	L
27	M	37	34	71	0.04	0.36	A
28	M	17	3	20	0.70	3.13	R
29	M	5	5	10	0.00	0.00	A
30	M	81	33	114	0.42	4.50	R
31	M	108	34	142	0.52	6.21	R
32	M	15	5	20	0.50	2.24	R
33	F	90	83	173	0.04	0.53	A
34	F	4	20	24	-0.67	-3.27	L
35	M	14	32	46	-0.39	-2.65	L
36	M	32	25	57	0.12	0.93	A
37	F	30	31	61	-0.02	-0.13	A
38	M	0	29	29	-1.00	-5.39	L
39	F	9	16	25	-0.28	-1.40	A
40	M	36	11	47	0.53	3.65	R
41	F	25	23	48	0.04	0.29	A

Test 2	R	L	N	LI	Z- score	Pref
29	12	41	0.41	2.65	R	
128	123	251	0.02	0.32	A	
53	46	99	0.07	0.70	A	
45	120	165	-0.45	-5.84	L	
73	135	208	-0.3	-4.30	L	
0	0	0	-	-	-	
49	54	103	-0.05	-0.49	A	
91	58	149	0.22	2.70	R	
94	94	188	0.00	0.00	A	
157	36	193	0.63	8.71	R	
21	51	72	-0.42	-3.54	L	
94	65	159	0.18	2.30	R	
22	19	41	0.07	0.47	A	
41	41	82	0.00	0.00	A	
29	39	68	-0.15	-1.21	A	
16	137	153	-0.79	-9.78	L	
88	37	125	0.41	4.56	R	
1	7	8	-0.75	-2.12	L	
88	22	110	0.60	6.29	R	
110	90	200	0.10	1.41	A	
24	43	67	-0.28	-2.32	L	

Table 2 (continued)

Test 2	R	L	N	LI	Z- score	Pref
8	110	118	-0.86	-9.39	L	
48	18	66	0.45	3.69	R	
31	74	105	-0.41	-4.20	L	
105	127	232	-0.09	-1.44	A	
39	49	88	-0.11	-1.07	A	
20	30	50	-0.20	-1.41	A	
113	134	247	-0.09	-1.34	A	
122	85	207	0.18	2.57	R	
10	1	11	0.82	2.71	R	
21	46	67	-0.37	-3.05	L	
5	20	25	-0.60	-3.00	L	
16	91	107	-0.70	-7.25	L	
83	44	127	0.31	3.46	R	
197	143	340	0.16	2.93	R	
3	56	59	-0.90	-6.90	L	
31	92	123	-0.50	-5.50	L	
25	35	60	-0.17	-1.29	A	
24	30	54	-0.11	-0.82	A	

individual level asymmetries in this task.

The datasets including age, sex, LI, Z-score, the number of left, right and overall of paw uses per animal and individual paw preferences were shown in Tables 2 and 3 for two tests.

3.1.3. Stability of individual preferences

In order to test whether individual cats showed stable side preferences, we assessed the first paw they used in each test. In test 1, 19 cats started with the right paw and 19 with the left paw and for 3 animals data was missing. Animals that started with the left paw had a significantly more negative LI (-0.25 +/- 0.52) than animals that started with the right paw (0.09 +/- 0.44) ($t_{(36)} = 2.21$; $p < 0.05$). Thus, individual preferences were stable in task 1. In test 2, there were 17 cats that started with the right paw and 23 that started with the left paw. Animals that started with the left paw had a significantly more negative LI (-0.28 +/- 0.40) than those that started with the right paw (0.10 +/- 0.36) ($t_{(38)} = 3.13$; $p < 0.01$). Thus, individual preferences were also stable in task 2.

Additionally, we also calculated correlation coefficients between the LI's obtained in the two tasks. There were significant positive associations between the LI obtained in task 1 with that obtained in task 2 overall ($r = 0.69$; $p < 0.001$), for lid opening ($r = 0.46$; $p < 0.01$) and for food handling ($r = 0.50$; $p < 0.01$). Therefore, individual side preferences in cats are stable and task-independent.

3.1.4. Task complexity and problem-solving ability

In order to assess whether one of the tasks was more complex, we compared average reaction time, and the total number of paw uses to solve the task between task 1 and task 2. Overall, cats needed significantly more paw uses to solve test 2 (113.34 +/- 76.94) than to solve test 1 (53.85 +/- 43.31) ($t_{(40)} = 5.62$; $p < 0.01$), indicating that task 2 was likely more complex for them to solve. However, there was no significant difference in reaction times between the two tasks ($p = 0.12$).

3.1.5. The relation between lateralization and problem-solving ability

In order to assess whether there was a correlation between individual strength of lateralization and problem-solving ability, we correlated absolute LI's as an indicator of individual lateralization strength with total paw use and reaction time (see Table 4). We found that cats that had stronger lateralization needed fewer paw uses for test 1 ($r = -0.42$; $p < 0.01$), as well as for test 2 overall ($r = -0.35$; $p < 0.05$) and test 2 lid opening ($r = -0.38$; $p < 0.05$). For reaction times, no significant effects between lateralized and ambilateral

Table 3

Individual paw preferences in cats for two different motor skills in test 2. [Sex: (F: female; M: male); Pref: paw preference (R: right paw; L: left paw; N: the overall number of paw uses per animal; A: ambilateral); LI: laterality index; Z-score: positive Z score values ($Z \geq 1.96$) indicate right lateral bias; negative Z-score values ($Z \leq -1.96$) indicate left lateral bias; -: value not calculated due to absence of paw intervention].

Cat	Sex	For opening the lid					
		R	L	N	LI	Z- score	Pref
1	F	3	36	39	-0.85	-5.28	L
2	M	26	11	37	0.41	2.27	R
3	F	60	47	107	0.12	1.26	A
4	F	29	33	62	-0.06	-0.51	A
5	F	21	44	65	-0.35	-2.85	L
6	M	72	84	156	-0.08	-0.96	A
7	F	0	0	0	-	-	-
8	F	40	38	78	0.03	0.23	A
9	F	65	0	65	1.00	8.06	R
10	M	71	85	156	-0.09	-1.12	A
11	F	95	36	131	0.45	5.15	R
12	M	21	26	47	-0.11	-0.73	A
13	F	67	37	104	0.29	2.94	R
14	F	17	16	33	0.03	0.17	A
15	M	15	28	43	-0.30	-1.98	L
16	M	27	5	32	0.69	3.89	R
17	F	16	78	94	-0.66	-6.39	L
18	M	88	37	125	0.41	4.56	R
19	F	1	7	8	-0.75	-2.12	L
20	M	56	18	74	0.51	4.42	R
21	F	110	90	200	0.10	1.41	A
22	M	24	43	67	-0.28	-2.32	L
23	M	13	24	37	-0.30	-1.81	L
24	M	8	52	60	-0.73	-5.68	L
25	F	46	13	59	0.56	4.30	R
26	F	26	9	35	0.49	2.87	R
27	M	74	105	179	-0.17	-2.32	L
28	M	12	10	22	0.09	0.43	A
29	M	20	30	50	-0.20	-1.41	A
30	M	75	111	186	-0.19	-2.64	L
31	M	81	74	155	0.05	0.56	A
32	M	10	1	11	0.82	2.71	R
33	F	17	28	45	-0.24	-1.64	A
34	F	5	20	25	-0.60	-3.00	L
35	M	14	30	44	-0.36	-2.41	L
36	M	53	43	96	0.10	1.02	A
37	F	112	95	207	0.08	1.18	A
38	M	3	26	29	-0.79	-4.27	L
39	F	31	50	81	-0.23	-2.11	L
40	M	19	30	49	-0.22	-1.57	A
41	F	22	30	52	-0.15	-1.11	A

For reaching food after opening the lid						
R	L	N	LI	Z- score	Pref	
3	0	3	1.00	1.73	A	
3	1	4	0.50	1.00	R	
68	76	144	-0.06	-0.67	A	
24	13	37	0.30	1.81	A	
24	76	100	-0.52	-5.20	L	
1	51	52	-0.96	-6.93	L	
0	0	0	-	-	-	
9	16	25	-0.28	-1.40	A	
26	0	26	1.00	5.10	R	
23	9	32	0.44	2.47	A	
62	0	62	1.00	7.87	R	
0	25	25	-1.00	-5.00	L	
27	28	55	-0.02	-0.13	A	
5	3	8	0.25	0.71	A	
26	13	39	0.33	2.08	R	
2	34	36	-0.89	-5.33	L	
0	59	59	-1.00	-7.68	L	
0	0	0	-	-	-	
0	0	0	-	-	-	
32	4	36	0.78	4.67	R	
0	0	0	-	-	-	

Table 3 (continued)

For reaching food after opening the lid						
R	L	N	LI	Z- score	Pref	
0	0	0	-	-	-	
0	0	0	-	-	-	
0	58	58	-1.00	-7.62	L	
2	5	7	-0.43	-1.13	L	
5	65	70	-0.86	-7.17	L	
31	22	53	0.17	1.24	A	
27	39	66	-0.18	-1.48	A	
0	0	0	-	-	-	
38	23	61	0.25	1.92	R	
41	11	52	0.58	4.16	R	
0	0	0	-	-	-	
4	18	22	-0.64	-2.98	L	
0	0	0	-	-	-	
2	61	63	-0.94	-7.43	L	
30	1	31	0.94	5.21	R	
85	48	133	0.28	3.21	R	
0	30	30	-1.00	-5.48	L	
0	42	42	-1	-6.48	L	
6	5	11	0.09	0.30	A	
2	0	2	1.00	1.41	A	

Table 4

Correlation between absolute LI's and problem-solving ability, ** $p < 0.01$; * $p < 0.05$.

Task	Dependent variable	Total paw use	Reaction time
Task 1	LI overall	-0.42**	-0.22
Task 2	LI overall	-0.35*	-0.25
	LI lid opening	-0.38*	-0.26
	LI food reaching	-0.26	-0.16

subjects were observed (all p 's > 0.1). For the three significant correlation coefficients, the distributions of individual data points were shown in Fig. 3–5.

In addition, we compared total paw uses, reaction times and the number of opened lids between lateralized and ambilateral animals. We found that lateralized animals opened significantly more lids successfully (3.88 ± 0.5) than ambilateral animals (3.27 ± 1.07) ($t_{(36)} = 2.07$; $p < 0.05$) in test 1. No significant differences between lateralized and ambilateral animals were observed for reaction times, and the total number of paw uses (all p 's > 0.36) in test 1 or any dependent variables in test 2 (all p 's > 0.26).

In an exploratory analysis, we, assessed whether head vs. paw preference when first interacting with the task apparatus had an impact on problem-solving ability. Regarding problem-solving ability, animals that directly used their paws opened more lids successfully in task 1 (3.83 ± 0.48) than those that started the task using their heads (3.07 ± 1.27) ($t_{(36)} = 2.65$; $p < 0.05$). The effects failed to reach significance for all other dependent variables in task 1 and all dependent variables in task 2 (all p 's > 0.05).

3.1.6. Effects of sex and sterilization on lateralization and problem-solving ability

We did not observe any sex effects on either lateralization nor problem-solving abilities (all p 's > 0.07).

Additionally, we also compared these variables between sterilized and non-sterilized animals. Here, we did again not observe any effects on LI's. However, several effects reached significance for problem-solving ability. Sterilized animals showed significantly less overall paw uses in both task 1 ($t_{(36)} = -2.37$; $p < 0.05$) and task 2 ($t_{(36)} = -2.75$; $p < 0.01$). Moreover, their overall reaction time in task 2 was considerably faster (246.86 ± 104.33) than that of not sterilized cats (375.20 ± 216.36) ($t_{(36)} = -2.41$; $p < 0.05$).

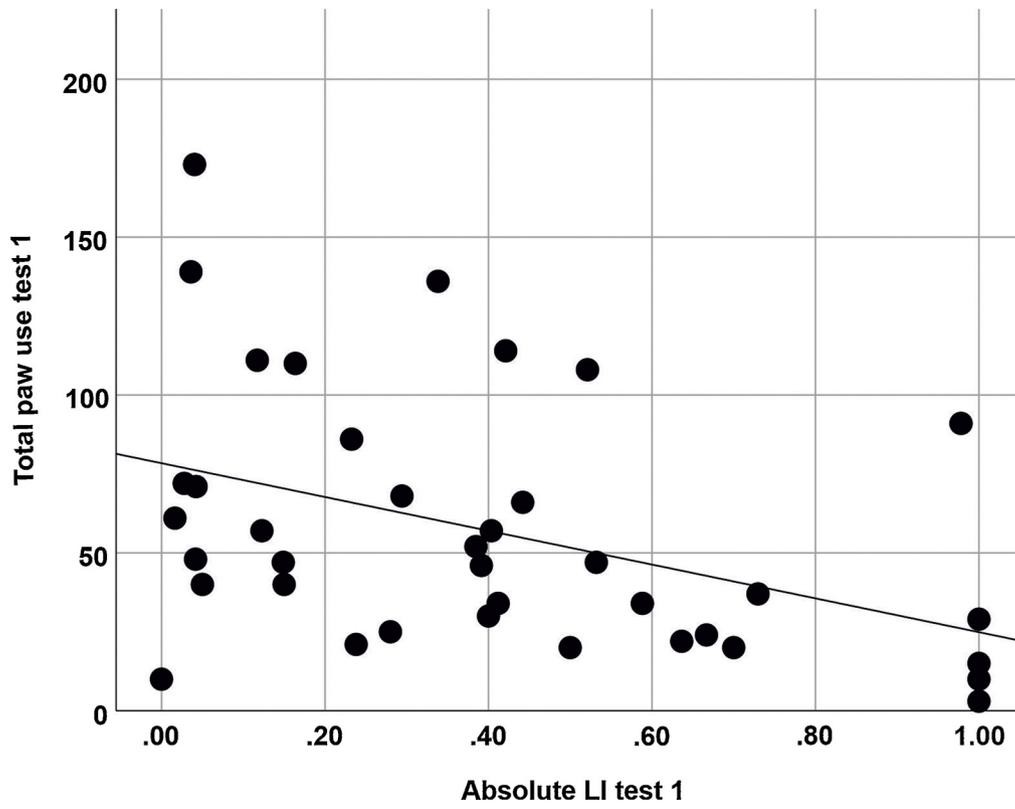


Fig. 3. Scatterplot showing the relation between the absolute LI and total paw use for test 1.

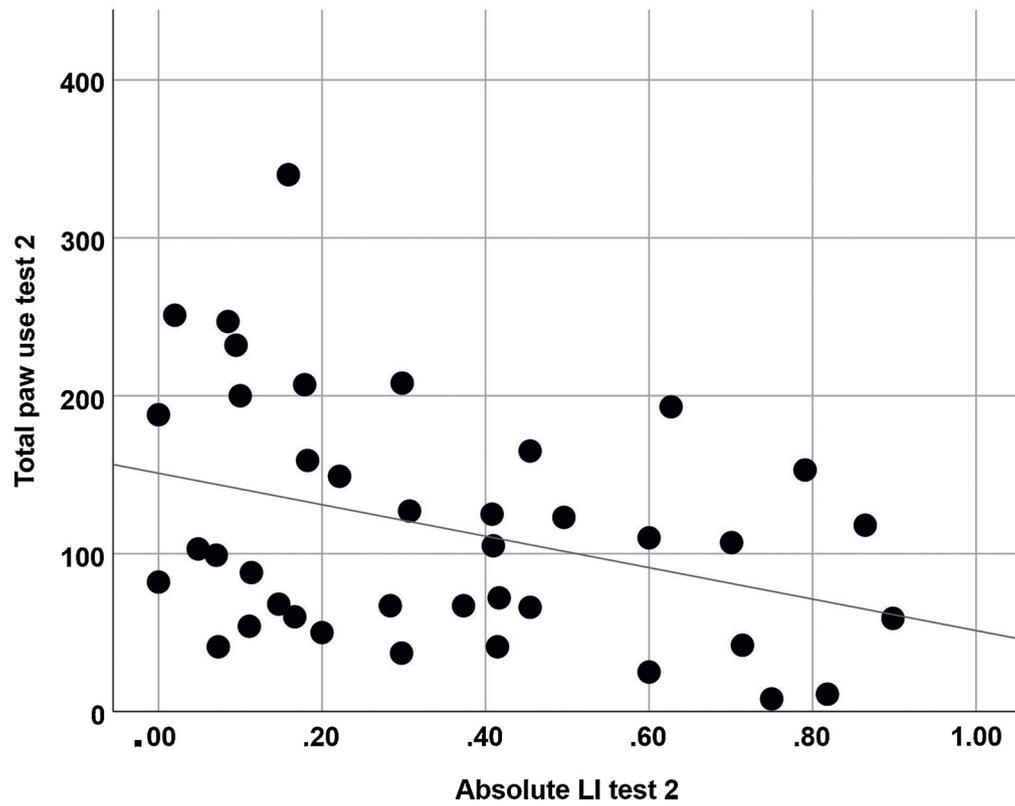


Fig. 4. Scatterplot showing the relation between absolute LI and total paw use for test 2.

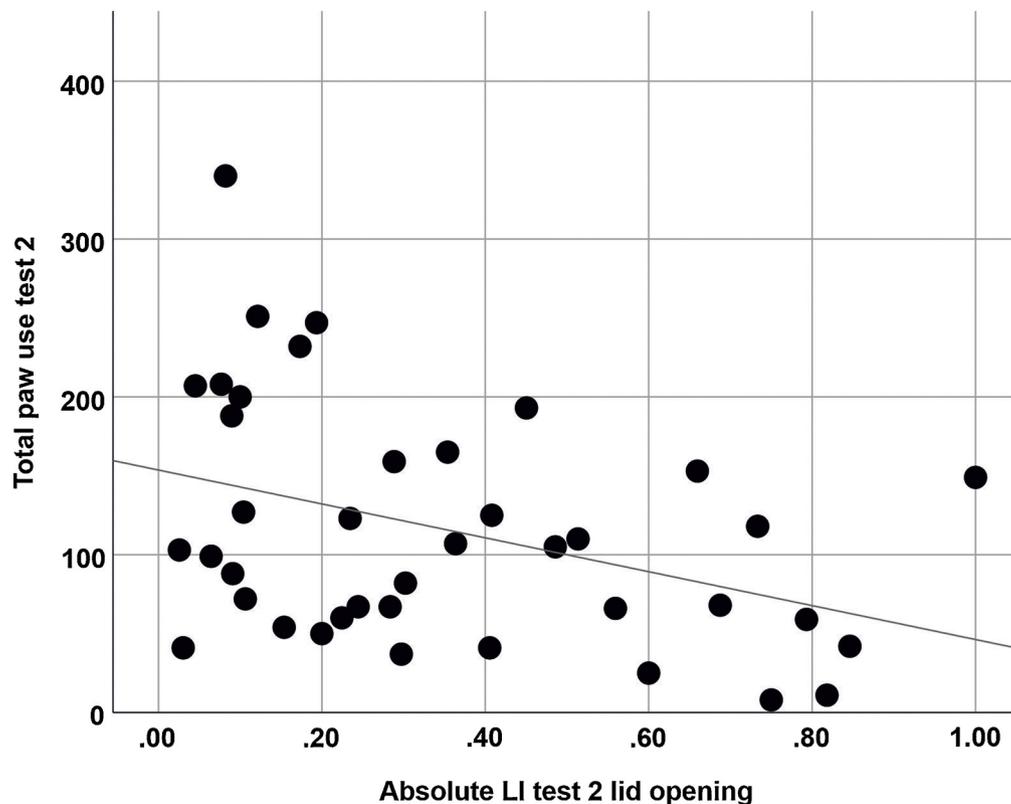


Fig. 5. Scatterplot showing the relation between absolute LI for lid opening and total paw use for test 2.

4. Discussion

This study was aimed to investigate the relationship between lateralization and problem-solving ability in domestic cats. Our findings show that cats with stronger lateralization need significantly fewer paw movements to solve the tasks. They also open significantly more lids during the tests. Thus, the strength of lateralization and problem-solving abilities are associated in domestic cats. Although cats have been evolved by human selection, they are still considered natural hunters [44]. In terms of genetic [45], morphological [46] and behavioural [47] patterns, domestic cats are considered to constitute a domestic species that is most similar to their ancestors. The innate feeding of the cats requires hunting (prey seeking, stalking and chasing) and scavenging [48] similar to their ancestral African wildcat [47]. Therefore, effective paw usage is extremely important for successful hunting and prey handling. Advanced cognitive abilities such as problem-solving, planning, self-control and learning may also have critical importance for species like cats adapted for hunting. Therefore, it is not surprising that cats with strong paw preference have higher motor and cognitive abilities. It is likely that the success of more lateralized animals was due to both higher motor dexterity and elevated cognitive ability since test 2 required to the cats learn different opening directions for each lid while a single direction was sufficient in test 1. Indeed, cats had longer reaction times in test 2, but both tasks showed a similar correlation between individual lateralization and task solving efficiency. In both tasks, correlation coefficients were negative, indicating that animals with stronger paw preferences needed fewer paw movements to solve the task. Thus, we assume that both motor and cognitive abilities were relevant to the success of the lateralized animals.

This is also consistent with previous studies suggesting that strength of laterality increases average cognitive ability in humans [49,50] as well as task-related efficacy in non-human primates such as marmosets [17] and chimpanzees [13]. Although these parallel findings can be explained by functional similarities in manipulating objects by paws/

hand in domestic cats and primates, the link between strength of laterality and performance was also shown in different species such as birds [14,16] and dogs [51]. Functional similarities between primates and domestic cats may further have relevant importance from a methodological perspective. We may expect that established methods in primate studies can easily be adapted to studies investigating motor laterality in cats. For instance, one of the main advantages of having strong laterality is suggested to have a better ability to detect predators. Considering the solitary living conditions of cats, strong laterality can also be important for cats to detect threats in the environment. Thus, further studies exploring strength of laterality in cats in a novel stimulus context may have particular importance in adding information on laterality in cats.

According to the strategy they initiated to solve the tests, cats were divided into two groups as head-preferring and paw-preferring groups. Interestingly, paw preferring cats opened more lids than the head-preferring ones. This suggests that paw-preferring cats have higher motor skills and possibly also higher problem-solving abilities than those having a head preference. One of the reasons for using the head rather than paw for the initial attempt to start the task might be the impact of the domestication process. This conclusion is based upon the literature that unlike the feeding and hunting rituals of wild cats, domestic cats are fed ad libitum from a bowl in a fixed position without requiring any manipulative motor skills [47]. This finding requires further investigation to provide greater insights into the usability of the paw and/or head preferences for an intelligence tool in cats.

In line with the meta-analyses on cat pawedness, the absence of a population bias and the presence of individual-level asymmetry in domestic cats was confirmed. Both findings are also in agreement with the meta-analysis, which reported that most cats have a greater preference to use their left or their right paw rather than being ambilateral [27]. It can reasonably be assumed that having a dominant paw for picking up a small prey is a significant advantage for cats which are opportunistic hunters.

To our knowledge, this is the first study examining the correlation between first and overall paw usage in cats. The results show that first paw preference and overall paw usage are significantly correlated, and this finding is in line with the results of a study indicating that the first-hand preference in the first trial is consistent with general hand preferences on two macaques [52]. However, contrary to previous studies showing that motor laterality is task-dependent [53–55], we observed that cats showed stable side preferences in both of the tests. However, it should be mentioned that both our tasks were, to some extent similar, although the animals had to adopt a different lid-opening strategy for each cup in test 2. Nevertheless, more research with a greater variety of tasks is needed in cats before any final conclusion can be drawn on task-independency of pawedness in cats. The explanation for both results may also be related to hunting behaviour in cats. From an evolutionary perspective, cats are different from humans, birds, dogs and further non-primate animals considering their limb functions. Cats are highly specialized to use their paws for hunting, holding and manipulating their prey [27,48,56–58]. Having a dominant paw for hunting small preys provides a critical advantage to cats as efficient hunters. Accordingly, cats may prefer to use their dominant paw in a diversity of tasks to increase their success rates. This result also has particular importance as one may assume that the direction of paw preferences in cats can be measured through simpler tasks and observations. Especially considering the difficulties of working with domestic cats, it is assumed that recording only first few paw usages rather than counting 50 or 100 paw usage is much more practical and it would make further studies easier.

Some studies have reported sex-dependencies of pawedness in cats [51,52, but see 20]. In the present study, the direction of the cats' motor bias was not found to be related to sex in either of the tests. Sterilization status of the cats was also investigated, and there was no relationship between sterilization status and laterality index. However, interestingly, sterilized cats utilized a significantly lower number of paw uses to achieve success in both tests. This finding might show that sex hormones have an impact on problem-solving ability in cats. The difference in performance between sterilized and non-sterilized cats might also be due to the differences in the care of their owners.

5. Conclusion

In summary, this study is the first to demonstrate a correlation between pawedness and problem-solving ability in cats. We also report that cats which directly used their paws to solve the problem were more successful than those which started the task using their heads. The direction of paw preferences was found to be stable across two different tests in cats. Moreover, it was also shown that the first paw preference for problem solving might be an indicator of overall paw preference of the cats. These results could be important for the ongoing development in the understanding of paw preferences stability in cats. Following further validation with larger amount of samples, problem-solving tests designed in the current study is promising to become a standard methodology in the near future.

CRediT authorship contribution statement

Sevim Isparta: Conceptualization, Investigation, Methodology, Writing - original draft. **Yasemin Salgirli Demirbas:** Investigation, Methodology, Writing - original draft. **Zeynep Bars:** Investigation. **Bengi Cinar Kul:** Writing - original draft. **Onur Güntürkün:** Methodology, Supervision, Writing - review & editing. **Sebastian Ocklenburg:** Data curation, Formal analysis, Writing - original draft. **Goncalo Da Graca Pereira:** Methodology, Supervision, Writing - review & editing.

Declaration of Competing Interest

There are no conflicts of interest to declare.

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