Assessment of Laterality in Companion Dogs: Within and Across Three Different Tests

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Abstract

Assessing behavioural lateralization, which reflects brain asymmetries, often involves observing the use of an animal's limb. In humans, this was referred to as handedness, whereas in canines, it was called pawedness. Over the decades, our understanding of lateralization extended significantly to encompass structural and functional differences among humans and non-human species. Recently, researchers began to recognize the inherently cooperative and uniquely trainable traits in canines, which made them an easier species to study. Moreover, canines and humans were found to share commonalities in many basic behavioural and functional traits. The study of laterality in canines, therefore, explored the potential for becoming a pathological model. However, measurements of canine pawedness lacked standardization and tended to focus on only one measurement method. This study investigated canine laterality by examining paw preference across three tests: The Kong Ball, V-Fence, and Puzzle Box Tests, each consisting of different tasks. A quantitative analysis approach was employed, focusing on paw preference as an indicator of lateralization, with the aim of exploring whether canines displayed consistent paw preferences across different tasks and the potential for generating a standardized pawedness test comprising multiple tasks. A total of 40 dogs were tested, and the results indicated that individual-level paw preferences were observed. Pearson Correlation analysis revealed that paw preference in the V-Fence Test was associated with paw use in The Kong Ball Test, suggesting some consistency in lateralization across tasks. However, no significant correlation was found between The Puzzle Box Test and the other tasks, which might have been attributed to differences in task complexity. The findings highlighted the need for further research to explore the possibility of integrating multiple methodologies to obtain a more comprehensive understanding of canine laterality.

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Abbreviations

LH = Left Hemisphere

RH = Right Hemisphere

5-HT = Serotonin

IAT = Intracarotid Amobarbital Testing

ASD = Autism Spectrum Disorder

G-G Theory = Geschwind and Galaburda's triadic theory

BORIS = Behavioral Observation Research Interactive Software

LI = Laterality Index

FRT = Food-reaching test

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I. Introduction

Laterality is defined as the preference for using homologous parts on one side of the body over the other, therefore typically showing lateral dominance function or characteristics in living organisms (de Jongh et al., 2022). Although in the context of cognitive neuroscience, laterality is often associated with functional specialization of the left and right hemispheres (Springer & Deutsch, 1997), it has a wide spectrum of applications, including body and organ asymmetries, cerebral asymmetries in brain structure, neurochemistry, and specialized function between the left and right hemispheres.

Cerebral asymmetry has been shown to correlate not only with many different functional expressions, such as handedness, eyedness, and footedness but also with cognitive differences like language and spatial ability. Furthermore, predispositions to certain psychopathological states, such as depression or schizophrenia, have been discovered to be associated with cerebral asymmetry as well. For a long time, laterality has been seen as especially exclusive to humans. A large part of the reason is that the study of lateralization began with understanding the brain and language ability (Ocklenburg & Güntürkün, 2018).

However, comparative neuroscientists have begun to explore the possible structural and functional differences in various species, including amphibians, birds, and mammals. Although mice and rats have been seen as the most frequently used vertebrate species in animal research (Isparta, 2023), plenty of studies have focused on canines due to the shared evolutionary history of mutual benefit and cooperation between canines and humans (Isparta et al., 2024). Identifying specific structural and functional lateralization in animals can provide insights into the psychological evolution of humans, as well as the cognitive and functional processes of closely related animal species (Isparta et al., 2024).

II. Structured Asymmetries

2.1 Somatic Asymmetry

Humans are classified as bilateral organisms in a broader sense because the human body develops along the anterior-posterior axis and the dorsal-ventral axis and expands toward the left and right (Corballis et al., 2021). However, many internal organs in the human body are not arranged in bilateral symmetry. For instance, the distinct placement of thoracic and abdominal organs is an example of organ asymmetry, namely situs solitus (Corballis et al., 2021). Most humans have the heart, stomach, spleen, and aorta on the left side, while the liver, gallbladder, and trilobed lung are on the right side (Corballis et al., 2021). Furthermore, the human skeleton shows structural asymmetry. A study demonstrates that the upper limb exhibits right biases in bone dimensions, including length and diaphysial breadth, while the lower limb shows left biases (Auerbach & Ruff, 2006). This result also indicates that there are biases in muscle mass distribution as well since skeletons and muscles collaborate in all kinds of motor movements. The study conducted by Marcin Lijewski and colleagues has demonstrated that asymmetry exists in muscle mass distribution and grip strength (Lijewski et al., 2021).

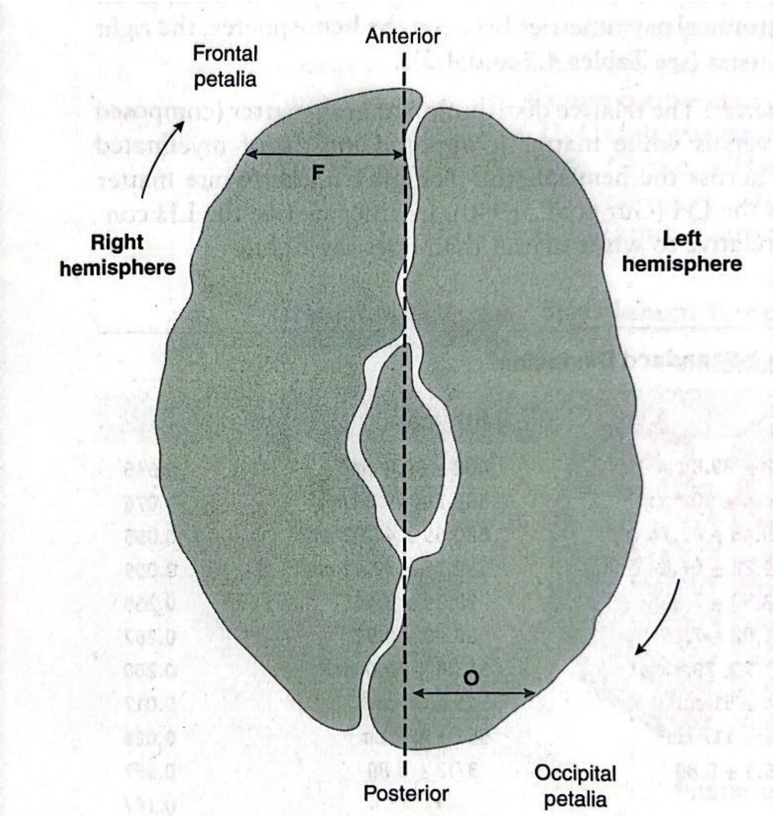
2.1.1. Cerebral Asymmetry

As one of the most important organs and the efficient centralized information processor, the brain exhibits many asymmetrical structural, neurochemical, and functional characteristics. Structurally, the left hemisphere (LH) has a longer frontal area, while the right hemisphere (RH) has a longer occipital area (See Figure 1.1). Additionally, the overall weight and volume in RH are greater than the LH as well. However, the LH has a greater grey matter/white matter ratio and cell packing density. Aside from that, cerebral asymmetries are also present in cortex thickness (Kong et al., 2018), connectivity (Thiebaut de Schotten et al., 2011), and gyrification

(Chiarello et al., 2016). The left and right hemispheres of the brain are not only asymmetrical as two halves but also contain specific structures that exhibit asymmetry as well, most of which can be observed before birth. Studies conducted on the asymmetry of temporal planum in early development in adults (Geschwind & Levitsky, 1968) indicate that the LH generally has a longer temporal planum among fetuses and adults (See Figure 1.2). This phenomenon can be observed in human fetuses as early as the 29th week of gestation (Bisiacchi & Cainelli, 2022).

Figure 1.1

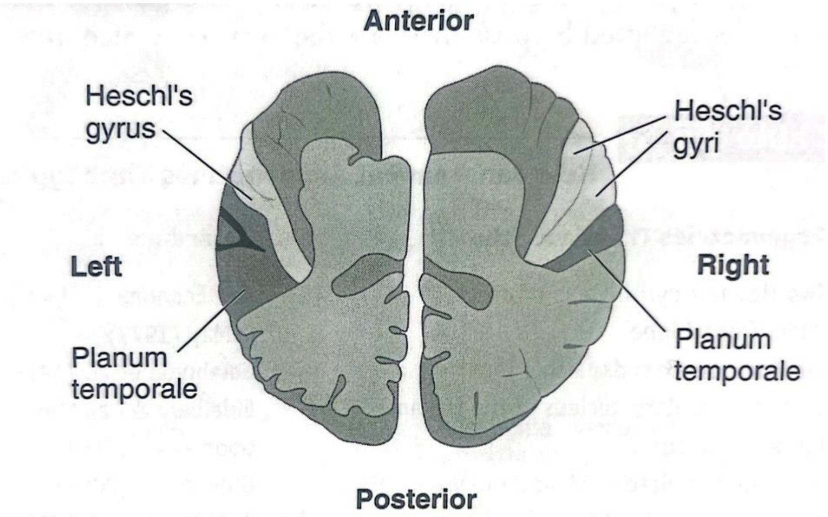
Asymmetry of the Brain Showing Frontal and Occipital Lobes



Note. From *Neuropsychology: Clinical and Experimental Foundations* (p. 109), by L. J. Elias, D. M. Saucier, 2006, Pearson/Allyn & Bacon. Copyright 2016 by Pearson Education, Inc.

Figure 1.2

Asymmetry of the Brain Showing Planum Temporale



Note. From *Neuropsychology: Clinical and Experimental Foundations* (p. 109), by L. J. Elias, D. M. Saucier, 2006, Pearson/Allyn & Bacon. Copyright 2016 by Pearson Education, Inc.

2.1.2. Neurochemical Asymmetry

Unlike neuroanatomical asymmetry, understanding the development of neurochemical asymmetry has been challenging because there are issues with generalization from animals to humans, and neurochemical asymmetries are typically regional, not hemispheric. Studies have revealed multiple neurotransmitters being distributed asymmetrically between regions of LH and RH. A study conducted in 1984 on rats indicated that the right accumbens has more dopamine and serotonin (5-HT), while the left accumbens has a higher 5-HT turnover (Rosen et al., 1984). Dopamine can also be found in the left globus pallidus in greater concentrations (Glick et al., 1982). Additionally, the concentration of norepinephrine has been shown to be greater in the right thalamus than in the left thalamus (Oke et al., 1978). Another study has demonstrated the existence of inter-hemispheric asymmetry in the mediofrontal region of the human brain (Arato et al., 1991). When considering neurochemical asymmetry, it is important to keep in mind that it is a dynamic concept, and all the processes interact and affect each other between LH and RH (Ramírez-Sánchez et al., 2021) and thus constitutes an asymmetric system that is related to behavioural lateralization and functional asymmetry.

III. Functional Asymmetries

1.1. Behavioural Asymmetry

As mentioned earlier, researchers have developed different paradigms to study human functional asymmetry. Most of them are investigations in behavioural lateralization, such as dichotic listening and tachistoscopic presentation (as described in Elias & Saucier, 2006). These paradigms focus on perception, such as auditory or vision. However, a comprehensive understanding of behaviour lateralization cannot be developed without considering another significant characteristic shown in humans, handedness, which has been studied for many decades.

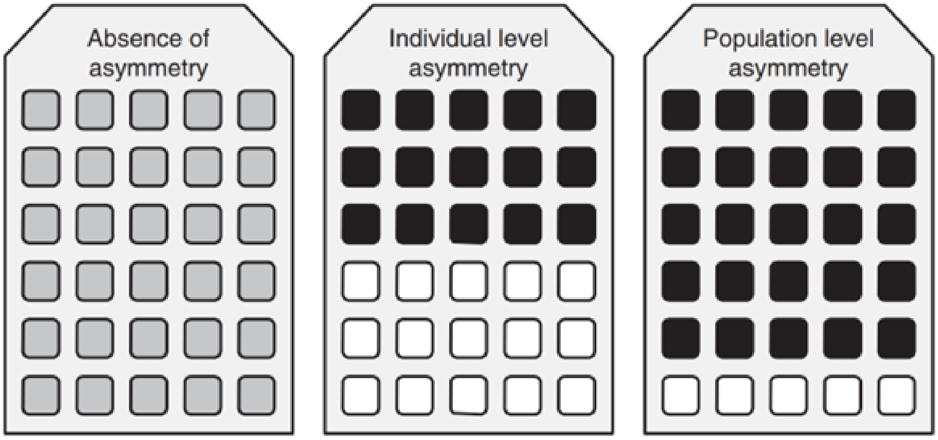
3.1.1. Handedness

Handedness is the most widely used indicator when investigating lateralization because it deeply reflects both motor performance and cognitive functions, including language and spatial ability (Brown et al., 2004). Like the previously discussed visual and auditory systems, the motor system exhibits contralateral organization, meaning that the right hand is mainly controlled by the LH, while the left hand is mainly controlled by the RH (Dragovic & Hammond, 2005). Three possible outcomes can be observed when testing any kind of limb preferences, including handedness: absence of asymmetry, individual-level asymmetry, or population-level asymmetry

(Ströckens et al., 2013). The differences between the three outcomes are shown in Figure 2. The absence of asymmetry indicates that all individuals in the population have an equal preference for using either the left or right limb (Ströckens et al., 2013). Individual-level asymmetry occurs when some individuals prefer the left limb while others prefer the right (Ströckens et al., 2013). Population-level asymmetry is characterized by a majority of the population showing a preference for either the left or right limb (Ströckens et al., 2013). A study suggested that the human left-hander and right-hander ratio around the world is roughly 1:10 (Papadatou-Pastou et al., 2020). Thus, it is a common agreement that most humans use their right hand as the dominant hand; in other words, humans showed a clear population level of asymmetry regarding handedness. Regardless of left-hander or right-hander, studies have also shown that the dominant hand is better at performing basic movement sequences like repetitive finger tapping (Hammond, 2002; Peters, 1980; Todor & Smiley-Oyen, 1987).

Figure 2

The three possible outcomes when testing limb preferences.



Note. Grey squares indicate individuals without a preference; black squares indicate individuals who prefer to use the right limb, and white squares indicate individuals who prefer to use the left limb. From “Limb preferences in non-human vertebrates,” by F. Ströckens, O. Güntürkün, and S. Ocklenburg, 2013, *Laterality: Asymmetries of Body, Brain and Cognition, 18:5,* 536-575, *(DOI: 10.1080/1357650X.2012.723008).* Copyright 2013 by Taylor & Francis.

3.1.1.1. Handedness and Language. The early studies of the brain mainly focused on gaining an understanding of the cognitive abilities of two hemispheres separately. Broca is the pioneer of functional specialization between LH and RH. His study demonstrated that LH is specialized in language, and RH is specialized in spatial ability, music, and other cognitive functions (as described in Elias & Saucier, 2006). However, according to Sperry and his colleagues, RH also accounts for some linguistic abilities, such as arranging letters to spell words and prosody (as described in Elias & Saucier, 2006). The relationship between handedness and language was not well studied until the invention of Intracarotid

Amobarbital Testing (IAT) by Juhn Wada. IAT is a procedure that involves temporary anesthesitizing one hemisphere of the brain to investigate expressive and receptive language ability. The analysis of IAT results indicates that language functions vary with hand dominance and that RH dominance for language can occur in the case of left-handers (as described in Elias & Saucier, 2006). However, all the studies are based on patients who undergo brain surgery. Thus, existing knowledge on the variability of language dominance is largely biased and influenced by pathological conditions. It is very prone to leading to a preconceived assumption that variations from LH language dominance are connected to brain abnormalities or left-handedness (Knecht et al., 2000).

3.1.1.2. Handedness and Spatial Ability. Over the years, researchers have focused on examining the correlation between handedness and intelligence. However, Ocklenburg pointed out that this field is full of exaggeration since left-handed people have been speculated to be more intelligent than right-handed people (Ocklenburg & Güntürkün, 2018). However, a meta-analysis conducted by Papadatou-Pastou and Tomprou (2015) showed no evidence of a higher prevalence of left-handedness among particularly intelligent individuals. Rather, they found a possible link between developing disorders and left-handedness in the case of intellectual disabilities (Papadatou-Pastou & Tomprou, 2015). Therefore, research on handedness and intelligence is considered valuable for advancing our understanding of developmental pathology and neurological disorders. Additionally, studying the possible relationship between handedness and specific cognitive functions can further deepen our knowledge of hemispheric asymmetries.

Interestingly, spatial ability is one of the major focuses regarding its relationship with handedness when considering specific cognitive domains rather than the overall intellectual level. Spatial tasks can be categorized into three main forms: spatial visualization, spatial orientation, and manual manipulation (Vogel et al., 2003). The spatial visualization task assesses the ability to mentally rotate objects, whereas the spatial orientation task evaluates the ability to respond to symbols arranged in various visual patterns. In contrast to these tasks, the manual manipulation task involves subjects physically responding to tactile stimuli organized in specific spatial patterns. Considering that spatial ability is mainly dominated by the RH, which also specializes in controlling the left hand, it is reasonable to hypothesize that left-handers will better solve spatial problems than right-handers. However, the lateralization on spatial ability could be task-specific; Vogel and colleagues (2003) conducted a meta-analysis study and found a right-hemisphere preference for the spatial orientation and the manual manipulation task but not for the spatial visualization task. The result supports the statement that the RH mainly dominates spatial ability but fails to demonstrate that left-handers will be better at solving spatial problems. Rather, Vogel (2003) reported a strong right hemisphere advantage for spatial tasks only in right-handers. This result may explain why another study has also found a small but significant advantage to the spatial ability of right-handers rather than left-handers (Somers et al., 2015). Additionally, sex interacts with handedness and impacts spatial ability as well. According to Sanders and his colleagues (1982), male left-handers had higher spatial scores than right-handers, whereas female left-handers had lower spatial scores than right-handers. Similar results were reported by several other studies (Annett, 1992; McGee, 1976).

3.1.1.3. Handedness and Task Complexity. When considering handedness, task complexity emerges as a crucial factor as part of the reflection of brain lateralization. An example of a simple task is grabbing food, while tasks requiring more cognitive abilities, such as problem-solving, are defined as complex tasks (Fagot and Vauclair, 1991). The complexity of the tasks has already been demonstrated to be associated with handedness. Williams and colleagues (2019) conducted a study that compared three different age groups of people on a series of tasks where the difficulties were increased. The result showed that task complexity significantly influences hand selection, particularly as the difficulty of a task increases (Williams et al., 2019). The more difficult the task, the more individuals tend to use the hand with better performance rather than the preference hand.

The relationship between limb preference and task complexity has been found not only in humans but also in several other species. Fagot and Vauclair (1991) introduced the Task Complexity Theory, which categorizes tasks into low and high levels based on their complexity in the non-human animal study. For high-level tasks, one of the most widely used standardized methods in laboratory settings is the tube task, which involves bimanual coordination (Caspar et al., 2018). Hopkins (1995) conducted a study on chimpanzees' hand use when extracting peanut butter from a tube and found evidence of right-handedness at the population level. Similarly, research on gorillas' manual signals indicated that behaviours involving communicative functions and social gestures are predominantly associated with the left hemisphere. This finding suggests that gorillas use their right hand more frequently during social behaviours compared to non-social activities, such as tool use (Prieur et al., 2017).

3.1.2. Measurements of Handedness.

When assessing handedness, how we define hand dominance is an important consideration. Researchers who studied motor performance define a dominant hand as playing an operational role more often, while the non-dominant hand is used to maintain stability (Guiard, 1987; Hammond, 2002). For instance, right-handers typically use their right hand to hold the pen and their left hand to stabilize the paper during writing tasks. Moreover, Humphrey proposed that an individual might prefer using one hand for certain tasks while being more skillful with the other (Corballis, M. C., 1983). Studies have also shown that the dominant hand is better at performing basic movement sequences like repetitive finger tapping (Hammond, 2002; Peters, 1980; Todor & Smiley-Oyen, 1987), which is mainly due to quicker and more consistent transitions between bending and straightening movements. Therefore, it is essential to distinguish between measures of preferences and performance. Generally, hand preferences are measured by questionnaires, while performance is measured using hand efficiency tests (Corballis, M. C., 1983). Questionnaires have been designed to encompass a wide range of ages, from preschoolers (Kastner-Koller et al., 2007) to adults (Byrne et al., 2004; Fazio et al., 2013; Prichard et al., 2013). The most common and widely used questionnaire is the Edinburgh Handedness Inventory (Prichard et al., 2013). The original inventory includes 20 questions on hand use (Oldfield, 1971), which have been reconsidered, with 10 questions finally being selected for a shorter version (Caplan & Mendoza, 2011). The questions used as indicators reflect a variety of functions, including drawing, writing, throwing, using scissors or toothbrushes, and so on (Caplan & Mendoza, 2011). The Fazio Laterality Inventory is a relatively new questionnaire (Fazio et al., 2013). It is inspired by the Edinburgh Handedness Inventory but also considers tasks that require precise hand motions, as well as social and communicative movements (Fazio et al., 2013). As two of the most well-known questionnaires, both consider hand dominance as a discrete measure by classifying individuals as left-handed, right-handed, or bilateral-handed. In addition, both inventories advocate that handedness should be evaluated over a series of tasks. Thus, a combination of assessments may be necessary for a more comprehensive understanding of laterality.

Although measuring performance between two hands is more complicated and time-consuming, it offers greater reliability than questionnaires, as discrepancies often exist between questionnaire responses and actual test results (Rigal, 1992). However, a major issue with performance-based assessments is the lack of standardized tasks. A study investigating six different measurements of hand preference and hand performance identified the Wathand Box as the most accurate predictor of hand preference (Brown et al., 2004). The Wathand Box is a series of performance-based tasks, including lifting a cupboard, using a toy hammer, tossing a ball, and so on. The test result was analytic using the laterality index calculated using the formula $(R - L)/(R + L)$ (Brown et al., 2004). Interestingly, regardless of questionnaires or performance tests, none of the assessments rely on a single task to determine handedness.

3.1.3. Other Measures of Laterality

Although handedness is the most extensively studied functional lateralization due to its strong association with language lateralization, it is not the only indicator when examining laterality (Tran et al., 2014). Other aspects include eyedness, footedness, and earedness. One of the most common methods for measuring these forms of lateralization is the use of questionnaires.

3.1.2.1. Eyedness. Eyedness refers to the tendency to favour one eye for tasks requiring the use of a single eye, such as viewing through a telescope (Tran et al., 2014). It is essential to distinguish eyedness from the test of sensory dominance, as it involves both eyes (Tran et al., 2014), it is also important to recognize the differences between eyedness and visual asymmetry. While eyedness is a behavioural preference, visual asymmetry is based on measurable differences in visual performance, such as variations in visual acuity and field of vision. The study on eyedness demonstrated that approximately two-thirds of the population have a dominant right eye (Bourassa, 1996). Another study has shown that eyedness is associated with handedness only in right-handed individuals and is also linked to visual acuity (Walter J. Friedlander, 1971).

3.1.2.2. Footedness. Footedness refers to the dominant or preferred foot used in different actions. This includes skilled movements like kicking a ball and stabilizing movements like standing on one foot (Tran et al., 2014). Interestingly, the population's preference for the right foot is significantly lower than for the right hand. This discrepancy is likely due to reduced social pressure. Meanwhile, some studies have suggested that footedness provides a better indication of cerebral lateralization compared to handedness. (Bryden, L. J. E. M. P., 1998; Elias et al., 1998; Searleman, 1980; Tran et al., 2014).

3.1.2.3. Earedness. Earedness refers to the preference for using one ear during monaural activities, such as pressing an ear against a closed door to eavesdrop on a conversation (Tran et al., 2014). Like eyedness, auditory asymmetry must be distinguished from earedness. Compared to handedness, eyedness, and footedness, earedness seems to be the least studied and the weakest lateral preference. Only approximately 60% of the population is right-eared (Tran et al., 2014).

3.2. Cognitive Asymmetry

Functional asymmetry can be investigated through cognitive tasks that assess different aspects of brain lateralization. Researchers have developed tasks that differentiate between verbal and nonverbal processing, local and global processing, high and low spatial frequency sensitivity, and high and low temporal frequency sensitivity (as described in Elias & Saucier, 2006). Verbal tasks typically engage the LH due to its superiority in linguistic processing, while nonverbal tasks engage the RH more. The concept of local versus global processing can be likened to focusing on individual trees versus the entire forest, with the LH better at recognizing local elements and the RH superior in identifying global elements (Fink et al., 1998). The spatial frequency hypothesis, which extends the local/global processing distinction to nonlinguistic areas, suggested that the LH is more sensitive to high spatial frequencies, while the RH shows sensitivity to low spatial frequencies (Jonsson & Hellige, 1986). Among these dichotomies, temporal frequency has gained broad acceptance and usage in research due to the substantial experimental evidence supporting it. However, there will always be ongoing debate regarding whether brain asymmetry should be conceptualized from a dualistic perspective (Fairweather et al., 1982).

Functional asymmetry can also be observed at a higher level of information processing. For example, researchers developed different paradigms to investigate auditory asymmetry and visual asymmetry. The most popular paradigm that is used to study auditory asymmetry is the dichotic listening task. Researchers simultaneously present two different auditory stimuli in each ear to explore the differences in the ability to process speech sounds between LH and RH (Hugdahl, 2005). The foundational study conducted by Kimura examined the correlation between auditory asymmetry and cerebral functional asymmetry. In this task, participants were presented with different auditory stimuli simultaneously in each ear. The result indicates that the right ear's superior word recognition reflects the left hemisphere's linguistic advantage, while the left ear's melody recognition ability demonstrates the right hemisphere's proficiency in perceiving melodic patterns (Kimura., 1967).

Vision asymmetry has been investigated largely using tachistoscopic presentations, a method that involves rapidly displaying visual stimuli to one visual field to study perceptual processing in the brain. Klein and colleagues (1976) discussed visual perceptual asymmetries in the recognition of words and faces using tachistoscopic tasks and found that right-handed individuals typically recognized more faces in the left visual field and verbalized more words in the right visual field during a simultaneous bilateral rapid serial visual presentation task.

3.3. Psychological Asymmetry

3.3.1. Neurodevelopmental Disorder - autism spectrum disorder (ASD)

Cerebral lateralization occurs during typical brain development, whereas atypical lateralization in brain structure and functions is considered to be associated with developmental disorders such as autism spectrum disorder (ASD). Individuals with ASD typically exhibit deficits in social and communication skills, along with stereotyped behavioural patterns (Ocklenburg & Güntürkün, 2018). Most studies that investigated the relationship between ASD and atypical lateralization primarily focused on handedness. A meta-analysis included 12 studies comparing handedness in the healthy group and the ASD group. The results indicated that compared to the healthy group, the ASD group showed a decrease in right-handedness and an increase in mix-handed and left-handed (Rysstad & Pedersen, 2016). Studies have also specifically focused on language lateralization to investigate and enhance our understanding of lateralization in relation to ASD, considering that a key characteristic of ASD is the impairment of communication abilities. Research on language lateralization has extensively used neuroimaging techniques to investigate brain activation patterns. One study analyzed the volumes of speech-associated gray and white matter, revealing that children with ASD exhibited atypical asymmetry in speech-related white matter structures, with significantly less left lateralization compared to typically developing children (Joseph et al., 2014). Another study measured regional cerebral blood flow—an indicator of brain region activation—while subjects were exposed to speech-like sounds (Boddaert et al., 2003). The findings demonstrated greater activation on the right side of the brain in individuals with ASD, whereas typically developing controls showed the opposite pattern, with more pronounced left-side activation (Boddaert et al., 2003).

3.3.2. Psychological Disorder - Schizophrenia

Schizophrenia is one of the most extensively studied mental disorders due to the severity of its symptoms and its lifelong prevalence and impact on individuals' well-being. Schizophrenia is characterized by delusions and hallucinations, as well as cognitive and motivational impairments (Ocklenburg & Güntürkün, 2018). Cognitive impairments include difficulties with attention and memory, while motivational impairments involve avolition, a lack of motivation to initiate and sustain goal-directed activities, and anhedonia, a reduced ability to experience pleasure.

The relationship between schizophrenia and atypical lateralization can be observed from the behavioural level and brain activation patterns. Researchers found that individuals with schizophrenia tend to be more non-right-handed than individuals without schizophrenia (Satz & Green, 1999). The gender effect, which arises from the higher likelihood of non-right-handedness in males compared to females and the greater prevalence of schizophrenia among males, was often seen as a confounding factor in the study of schizophrenia and handedness. The result of the existence of non-right-handedness in schizophrenia was confirmed by two other meta-analysis studies that have ruled out the potential influence of gender (Dragovic & Hammond, 2005; Hirnstein & Hugdahl, 2014). Additionally, individuals with schizophrenia were also found to have less left-hemispheric dominance in language tasks (Ocklenburg & Güntürkün, 2018). In the meta-analysis studies, the analysis of the data from dichotic listening studies showed a reduced right-ear advantage for individuals with schizophrenia (Ocklenburg et al., 2013; SOMMER et al., 2001). Studies using neuroscientific techniques like EEG or fMRI have found more supportive evidence (Alary et al., 2013; Angrilli et al., 2009).

IV. The Theories of Laterality

Along with studies investigating human lateralization and handedness, there has been a growing interest in hypothesizing its origins and evolution. Numerous theories have been developed to explain the origin of laterality, encompassing four main aspects: environmental, genetic, anatomical, and developmental. Jackson and Blau focused on the environmental explanation of handedness. Jackson’s Parental Pressure Theory and Blau’s Psychodynamic Theory both propose that handedness results from environmental factors and is entirely determined by a child's surroundings (as described in Elias & Saucier, 2006). However, the biggest issue with environmental explanation is the Adoption studies. Adoption studies investigating the handedness of children, their biological parents, and their adoptive parents revealed that a child's handedness is more closely related to their biological parents (as described in Elias & Saucier, 2006). This finding suggests that genetic factors play a significant role in handedness. Many genetic theories consider handedness to be a recessive trait, following Mendelian law. However, this genetic model is found to be too simple to explain the inheritance of left-handedness. Therefore, to gain a better understanding of left-handedness, researchers also focused on the Genetic-Environmental Interactions Model. For instance, Annett proposed a model to predict the emergence of various handedness patterns. Despite the fact that her model aligns well with most of the data, it presents significant challenges in terms of testability (Bryden, M. P., 1982). Additionally, theories emphasizing anatomical factors offer a surprisingly compelling perspective. The sword and shield theory proposed by Thomas Carlyle suggested that the position of the left hand is physiologically predisposed to protect the heart due to its position on the left side of the body. Consequently, the right hand is designated to hold the sword and attack enemies (as described in Elias & Saucier, 2006).

Among all the aspects, developmental theories are the most comprehensive, as they incorporate a wide range of factors rather than focusing only on handedness. One of the most popular theories is Geschwind and Galaburda's triadic theory (G-G theory), which suggests that increased testosterone levels are accountable for deviations from the typical dominance pattern (as described in Elias & Saucier, 2006). The G-G theory also claims that there is a correlation between handedness and immune disorder (as described in Elias & Saucier, 2006). Additionally, some other evolutionary theories provide valuable insights into the lateralization processes in infants since studies have demonstrated that the fetus exhibits lateralization from 10 weeks of gestation (Hepper, 2013). Studies on fetal position revealed that the asymmetries in the auditory system are attributed to the fetus typically having the right ear facing outward (as described in Elias & Saucier, 2006). Meanwhile, it is essential to realize that the methods used to measure lateralization in newborns differ from those used with adults and older children, as it is impossible to ask infants to identify words they heard in a dichotic listening task or answer questionnaires. Given that both infants and animals are non-verbal, some methods used to measure laterality in infants have inspired comparative researchers to develop similar measurements for assessing laterality in animals.

V. Laterality in Animal Kingdom

Interestingly, humans are not the only species that show asymmetry. Biologists reported findings in morphological asymmetry as well as behavioural lateralization across species.

Morphological asymmetry can be divided into dextral and sinistral (Palmer, 2009). Dextral indicates right-sided, while sinistral indicates left-sided. The study examined the directions of coiling in Gastropods and demonstrated a predominantly coiling preference toward the right (Gould & Young, 1985). Moreover, the narwhal’s tusk is found to be significantly predominant in sinistrally-coiled (Palmer, 2009). Further investigations of asymmetry presentation revealed evidence of both fixed and random asymmetries. Researchers defined fixed asymmetries as the overwhelming display of unilateral lateralization in the same species, whereas random asymmetry appears when dextral and sinistral forms are both common in one species (Palmer, 2009).

While studies on laterality have extensively focused on humans and observed morphological predominance across the animal kingdom, there has been a recent shift towards examining behavioral asymmetry in animals. Behavioral lateralization, a widely studied area, provides valuable insights into cerebral asymmetry due to the contralateral organization of all vertebrates, including humans. Research in this field spans a diverse range of species, from fish (Chivers et al., 2017) and reptiles (Bisazza et al., 1998) to mammals (Versace et al., 2007). Many studies on behavioral lateralization in animals are closely related to or based on human research. For instance, studies have shown that the left hemisphere (LH) of animals is typically responsible for routine tasks such as finding food and processing familiar, species-typical vocalizations, while the right hemisphere (RH) is associated with expressing negative emotions and social behaviors (Rogers, 2010).

VI. Laterality in Canines

Among all animals, dogs are the first domesticated species (Perri et al., 2021) and a frequent choice for human companionship, making them a primary research focus. Studies have demonstrated that canines have developed anatomical and behavioural adaptations to better communicate with humans (Kaminski et al., 2019). For example, dogs have developed a muscle specifically responsible for raising the inner eyebrow, which is consistently present in dogs but not in other species, including wolves, their closest relatives (Kaminski et al., 2019). Furthermore, the behavioural adaptations of dogs, such as the ability to effectively interpret human communication cues like hand gestures and gaze direction, make them inherently cooperative and uniquely trainable (Kaminski et al., 2019). As a result, preparing a dog for an experiment is generally easier than other species (Isparta et al., 2024).

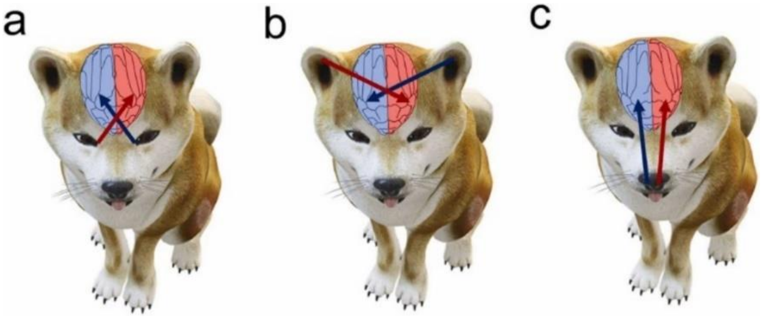
Moreover, studies on dogs have demonstrated that dogs and humans share many basic behavioural and functional traits and skills, including pathological mechanisms associated with mental illness (Overall, 2000; Starkey et al., 2005). Consequently, dogs have become valuable for investigating specific aspects of human social-cognitive evolution in comparative neuroscience. Similar to human studies, canine laterality research can be examined from functional and psychological perspectives.

6.1. Functional Aspects

Studies of the functional laterality in Canine have been done across different sensory modalities such as vision, olfaction, and audition. As mentioned before, vertebrates have contralateral organization, meaning that sensory input from one side of the body is primarily processed by the other side of the brain. Similar to humans, the sensory input pathway of vision and audition in canines follows the contralateral organization, while the nerve fibres in the olfaction pathway are connected to the corresponding side of the brain (See Figure 3). Research on canine vision has investigated visual preferences during agility-jumping tasks by alternately blindfolding the dogs' left and right eyes (Siniscalchi et al., 2017; Tomkins et al., 2010a). Additionally, studies have examined head-turning responses to visual stimuli presented during feeding behaviour (Siniscalchi et al., 2010). Olfactory studies focused on using the left and right nostrils in free-sniffing situations (Siniscalchi et al., 2011; Wells., 2003). Auditory studies focus on the dog's response to the different communicatory components of human speech (Andics et al., 2017; Ratcliffe & Reby, 2014). However, it is important to realize that the way we view canine sensory modalities may be oversimplified. For instance, in Figure 3a, only the optic neurons exhibiting a contralateral organization, where they cross over to the opposite side of the brain, are depicted. However, it is important to note that there is also a set of optic neurons that follow an ipsilateral pathway, remaining on the same side of the brain.

Figure 3

Organization of the Canine Nervous System



Note. From “Testing of behavioural asymmetries as markers for brain lateralization of emotional states in pet dogs: A critical review,” by T. Simon et al., 2022, *Neuroscience and Biobehavioral Reviews*, *143*, 104950 (*DOI: 10.1016/j.neubiorev.2022.104950*). Copyright 2022 by The Author(s)

6.2. Psychological Aspects

So far, most studies that have investigated the psychological aspects of canine laterality have focused on how laterality is related to emotional states and temperament, yet there are challenges. One primary difficulty is defining emotions and personality traits in canines, as they cannot provide linguistic feedback to describe their emotions and personalities. Thus, studies on emotions have depended mostly on nonverbal indicators like behavioural measures to understand the emotional process (Simon et al., 2022). Moreover, researchers have also used indicators including physiological and endocrinological measures such as heart rate, cortisol concentrations and so on (Simon et al., 2022).

6.2.1. Emotional States

Interestingly, functional behaviours that have been discussed can be analyzed to indirectly study cerebral asymmetries under emotionally relevant conditions. For instance, when a dog perceives a stimulus as emotionally significant, it might primarily examine it with one of each sensory organ (eye, ear, or nostril) or exhibit asymmetrical motor behaviour in response to the stimulus (Simon et al., 2022). The visual study conducted by Siniscalchi and colleagues on head-turning responses to pictures of snakes and cats found that alarming stimuli are processed dominantly by the left eye or the RH (Siniscalchi et al., 2010). Results from other studies supported the conclusion by using pictures with threatening faces from other dogs and humans (Barber et al., 2016; Racca et al., 2012). The olfactory study conducted by Siniscalchi and colleagues demonstrated that the RH processes the odour of veterinary sweat and adrenaline (Siniscalchi et al., 2011). Additionally, Siniscalchi and colleagues have also found that the sounds of thunderstorms are predominantly processed by RH, while the LH processed vocalizations for another dog (Siniscalchi et al., 2008). Aside from functional behaviours, tail wagging has also been an interesting indicator. Multiple studies have found that dogs' tails wagged more to the right when familiar individuals approached but more to the left when unfamiliar individuals approached (Laverack et al., 2021; Quaranta et al., 2007; Siniscalchi et al., 2017). All the results indicated that fearful emotions in dogs are processed dominantly by the RH, which implies that the RH deals mainly with negative emotions (Summarized by Leliveld et al., 2013).

6.2.2. Temperament

Most studies on canine temperament measurements are for dog selection and training (Batt, Lara S. et al., 2008). Because temperament tests are designed to select working dogs or dogs that need to be re-homed from shelters, most rely on questionnaires developed for puppy raisers or owners. However, research on lateralization and fear explores the connection between lateralization and temperament. One study indicated that ambilateral dogs are more likely to show distress in response to thunder and fireworks (Batt, Lara S. et al., 2008). In other words, dogs with less lateralization are more susceptible to stress. Another study provides supporting evidence by demonstrating that higher levels of lateralization are associated with dogs exhibiting more confident and relaxed behaviour when exposed to novel stimuli and unfamiliar environments (Batt, Lara S. et al., 2008). Studies have also shown that acute and chronic stress correlates with am-bilaterality in dogs (Demirbas et al., 2023; Demirbas et al., 2019). Given that distress response is an unwanted trait in working/service dogs, studying lateralization can help design a comprehensive temperament test that is considered objective and subjective. A study using the questionnaire, and the behavioural laterality test found lateralized dogs scored slightly higher on measures of stranger-directed aggression than ambilateral dogs (Schneider et al., 2013).

6.3. Pawedness

Similarly to handedness in humans, pawedness is an essential indicator of lateralization in dogs; it is described as the preference for using one side of the limb to complete specific tasks and is also known as paw preferences (Tomkins et al., 2010a). However, unlike studies on human laterality, research involving dogs cannot rely on questionnaires. The primary challenge is to define right-pawed and left-pawed tendencies in dogs and to develop a standardized behavioural test that can reliably measure pawedness in dogs. A variety of tasks have been tested in the study of paw preferences over time, including removing tape from eyes (Tan, 1987) and nose (Quaranta et al., 2004), obtaining food from a tube (Laverack et al., 2021), stabilizing the Kong (Branson & Rogers, 2006; Wells et al., 2016) or toy balls (Branson & Rogers, 2006; Poyser et al., 2006), paw lifting or taking the first step (Tomkins et al., 2010b). Among all methods, four paradigms are considered relatively reliable: the Tape Test, the Kong Ball Test, the Paw Lift Test, and the First-Stepping Test (Wells et al., 2018).

6.3.1. Measurements of Pawedness.

6.3.1.1. The Tape Test

The first tape test was conducted by Tan in 1987; an adhesive plaster was used to cover the dog’s eyes (Tan, 1987). The dog was allowed to attempt to remove the plaster using its right or left paw. However, this procedure had to be repeated 100 times, which could lead to a negative experience for the dog. The result of the study indicated a strong preference for right paws in dogs on a general group level (Tan, 1987). A study by Quaranta in 2004 improved The Tape Test by setting up a 2-minute timeframe, reducing the time for the dog to repeat the test. Quaranta collected data on the first paw used to remove the tape and focused on the total number of attempts (Quaranta et al., 2004). The result of the study showed a population lateralization among dogs, which provides supportive evidence for Tan’s conclusion. Quaranta then did another study in 2006 using the exact same method to investigate lateralized behaviours and immune responses in dogs (Quaranta et al., 2006). The results showed that paw preferences could affect the immune response in dogs. More specifically, left-pawed dogs exhibited lower titers of anti-rabies antibodies compared to right-pawed and ambidextrous dogs, their serum levels of interferon-γ were also reduced relative to both right-pawed and ambidextrous dogs (Quaranta et al., 2006). Additionally, Poyser (2006) further streamlined the procedure by reducing the number of tests to 20. However, the result of the study failed to show any significant population tendency towards a right- or left-paw preference (Poyser et al., 2006). This might be due to an insufficient number of data points collected. Thus, Batt increased the data points to 26 when designing a subsequent study in 2007. Nonetheless, the study failed to report paw preferences using The Tape Test (Batt, Lara et al., 2007). Despite Well's attempt to measure paw preference using The Tape Test with an increased number of data points (50), he encountered the same challenges. Both studies reported severe data loss due to the dogs' frantic behaviours during the tape removal process, such as rubbing their faces against walls, spinning, and rolling on the floor (Batt, Lara et al., 2007; Wells et al., 2018). The various studies and designs are summarized in Table 1.

Table 1

A list of Studies Illustrating the Development of the Design of The Tape Test.

Publication	Method	Data collection	Data analysis
Tan (1987)	The dog’s eyes were covered with adhesive plaster. Then, the dog is	100 (total number of right and left paws)	The binomial test for large samples was calculated (the significance of the difference in frequencies

	allowed to attempt removing the plaster using its right/left paw. The frequency of paw use was recorded for each paw, with a score assigned for the right paw and a separate score for the left paw.		between right and left paw usage)
Quaranta et al. (2004)	An adhesive tape of three various sizes (19 mm × 38 mm; 10 mm × 20 mm; 5 mm × 10 mm, adjusted for different animal sizes) was applied longitudinally along the midline of the nasal bridge.	i) The first paw used in attempts to remove the tape ii)The total number of attempts made with the left and the right paw in the 2 min of test duration.	$\frac{\#of\ times\ the\ left\ paw\ was\ used\ first}{\#\ of\ times\ the\ left\ paw + \#\ of\ times\ the\ right\ paw} \times 100$ $\frac{Total\ \#\ of\ times\ for\ left\ paw}{Total\ \#\ of\ times\ for\ left\ paw + Total\ \#\ of\ times\ for\ right\ paw} \times 100$
Quaranta et al. (2006)	Used the same procedure as Quaranta et al. (2004)	The same as Quaranta et al. (2004)	The same as Quaranta et al. (2004)
Poyser et al. (2006)	The same procedure as Quaranta et al. (2004) except for the size of the tape (2 cm × 2cm)	Data collection continued until around 20 tests had been conducted or when dogs became distressed	The handedness index (HI) was calculated using the formula HI = (frequency R − frequency L)/total frequency.
L. Batt et al. (2007)	The position of the tape is the same as Quaranta et al. (2004). The size of the tape is 15 mm × 50 mm.	Collect 26 paw-use data points (Left + Right).	The Laterality index (LI) of motor preference was calculated using the formula: (SR – SL)/(SR + SL) × 100. (SR is the number of times the right paw is used, and SL is the number of times the left paw is used.) The absolute value of LI was calculated.

			The binomial z-scores were calculated using the formula: $Z = (SR - [(SR + SL)/2)]/\sqrt{}[(SR + SL)/4]$
L. Batt et al. (2008)	The same procedure as L. Batt et al. (2007)	The same as L. Batt et al. (2007)	The same as L. Batt et al. (2007)
L. S. Batt et al. (2009)	The same procedure as L. Batt et al. (2007)	The same as L. Batt et al. (2007)	The same as L. Batt et al. (2007), except for the expression of the LI formula. $LI = \frac{R-L}{R+l} \times 100$
Wells et al. (2018)	The same procedure as L. Batt et al. (2007)	Collect 50 paw-use data points (Left + Right).	Binomial z-scores were calculated.

6.3.1.2. The Kong Ball Test

In The Kong ball Test, each dog was given a hollow Kong filled with food and placed on a flat surface. Paw use was characterized as the dog's preference of either its left, right, or both paws to hold the Kong ball in position throughout the test (Batt, Lara S. et al., 2008). Branson and Rogers (2006) conducted the first Kong Ball Test study. In this study, 48 dogs were observed, and 100 examples of paw use were recorded for each dog. Each time a paw left the Kong ball, it was counted as a single paw use. A subsequent study investigated whether recording 50 paw uses would be sufficient to draw conclusions comparable to those obtained from 100 paw uses (Batt, Lara et al., 2007). This study confirmed that recording 50 instances of paw use is sufficient, saving resources and time for further research. Nevertheless, none of the Kong Ball Tests conducted so far have reported a significant population lateralization bias overall, with lateralized and non-lateralized individuals evenly distributed across the population (Marshall-Pescini et al., 2013; McGreevy et al., 2010; Tomkins et al., 2010a; Wells et al., 2018). For complete studies and designs, see Table 2.

Table 2

A list of Studies Shows the Development of the Design of the Kong Ball Test.

Publications	Method	Data collection	Data analysis
Branson & Rogers (2006)	A large classic Kong was used. It is a hollow, conical rubber tube measuring 10 cm long, featuring a 10-mm hole at one end and a 25-mm hole at the opposite end. The Kong was filled with chicken and rice sausage meat and presented to the dog on a flat surface.	The use of the left/right or both paws to hold the Kong while interacting was recorded. 100 (L + R) data points were collected from each dog.	Binomial z-scores were calculated using the formula, $z = \frac{R-0.5N}{\sqrt{0.25N}}$, where R = the number of right paw uses and N = the sum of left and right paw uses. Handedness Index (HI) was calculated by (L – R/L + R)
L. Batt et al. (2007)	A similar Kong was used by Branson & Rogers (2006). However, filled with liver, beef, lamb, chicken, and peanut butter was used. An Alternative Kong, filled with soft cat food, was prepared for dogs that showed disinterest.	The same as what Branson & Rogers (2006) did. 100 (L + R) data points were collected from each dog.	Fifty data points and 100 data points were compared, and no differences were found. The Laterality index (LI) of motor preference was calculated using the formula: (SR – SL)/ (SR + SL) × 100. (SR is the number of times the right paw is used, and SL is the number of times the left paw is used.)

			The absolute value of LI was calculated. The binomial z-scores were calculated using the formula: $Z = (SR - [(SR + SL)/2)]/\sqrt{}[(SR + SL)/4]$
L. Batt et al. (2008)	The same procedure as L. Batt et al. (2007).	Similar to L. Batt et al. (2007), 100 (L + R) data points were collected from each dog.	The expression of the LI formula has changed to $LI = \frac{R-L}{R+L} \times 100$. Used the same binomial formula that used by Branson & Rogers (2006).
Siniscalchi et al. (2008)	The same procedure as what Branson & Rogers (2006) did. Filled the Kong with meat and dry dog food.	Based on L. Batt et al. (2007)'s finding, only 50 (L + R) data points were collected.	The same analysis as Branson & Rogers (2006). $z = \frac{R-0.5N}{\sqrt{0.25N}}$
L. S. Batt et al. (2009)	The same procedure as L. Batt et al. (2007)	Similar to L. Batt et al. (2007), 100 (L + R) data points were collected from each dog.	The LI formula was used by L. Batt et al. (2008). $LI = \frac{R-L}{R+L} \times 100$
Tomkins et al. (2010b)	Followed the procedure described by L. Batt et al. (2007) with different fillings in the Kong.	Based on L. Batt et al. (2007)'s finding, only 50 (L + R) data points were collected.	The same analysis and formula were used by L. Batt et al. (2007).

McGreevy et al. (2010)	The same procedure was used as Branson & Rogers (2006) did with the same filling.	The same as what Branson & Rogers (2006) did. 100 (L + R) data points were collected from each dog.	Used the same LI formula as L. S. Batt et al. (2009). Calculated the binomial z scores using L. Batt et al. (2007)’s formula. $Z = (R - [(R + L)/2)]/\sqrt{}[(R + L)/4]$
Marshall-Pescini et al. (2013)	Followed Branson Rogers's (2006) procedure, except for filling a medium Kong with canned meat and rice.	The same as what Branson & Rogers (2006) did. 100 (L + R) data points were collected from each dog.	HI was calculated in the same way as what Branson & Rogers (2006) did. HI = (L – R/L + R)
Wells et al. (2016)	Followed Branson Rogers's (2006) procedure, except for filling a medium Kong with canned meat and rice.	The same as what Branson & Rogers (2006) did. 100 (L + R) data points were collected from each dog.	Binomial z-scores were calculated, but the formula used was not mentioned.
Siniscalchi et al. (2016)	Followed a modified Branson Rogers's (2006) procedure. Two Kong sizes were used for different dogs. A 15-minute timeframe was used for each dog.	Based on L. Batt et al. (2007)’s finding, only 50 (L + R) data points were collected.	Laterality Index (LI) was calculated using $\frac{Total\ \#\ o}{Total\ \#\ of\ times\ for\ left}$ 100
Wells et al. (2017)	A medium classic Kong was used. It is a hollow, conical rubber tube measuring 10.5 cm long, featuring a 2.9	The same as what Branson & Rogers (2006) did. 100 (L + R) data points were	Binomial z-scores were calculated, but the formula used was not mentioned. HI was calculated in the same way as

	cm hole at one end and a 1 cm hole at the opposite end. The Kong is filled with moist dog food.	collected from each dog.	what Branson & Rogers (2006) did. HI = (L – R/L + R)
Wells et al. (2018)	The same procedure as Wells et al. (2017).	The same as what Branson & Rogers (2006) did. 100 (L + R) data points were collected from each dog.	The same analysis was used by Wells et al. (2017). The absolute LI was calculated.
Simon et al. (2022)	Followed the procedure described by L. Batt et al. (2007) and Tomkins et al. (2010).	Based on L. Batt et al. (2007)’s finding, only 50 (L + R) data points were collected.	Modified Branson & Rogers's (2006) HI formula by changing HI to LI. Thus, the formula became LI = (L – R/L + R) The absolute value of LI was calculated.
Demirbas et al. (2023)	The measures of the Kong ball were unknown. Two Kong sizes (Large and small) were used for different dogs. Wet dog food was used to fill the Kong.	Based on L. Batt et al. (2007)’s finding, only 50 (L + R) data points were collected.	The same formula was used by L. Batt et al. (2008) when the LI was calculated. $LI = \frac{R-L}{R+L} \times 100$ The binomial z-scores was calculated using the same formula as Branson & Rogers (2006). $z = \frac{R-0.5N}{\sqrt{0.25N}}$

6.3.1.3. The Paw-Lifting Test

Research on lateralization through paw lifting is significantly less common compared to other paradigms. In The Paw-Lifting Test, the dog was instructed to sit and raise one of its paws under the experimenter's guidance (Wells, 2003). The first paw that the dog lifted was recorded as a single paw use. Wells identified potential shortcomings of the paw-lifting experiment after several investigations (Wells, 2003; Wells et al., 2018). The act of lifting a paw, being a basic repetitive behaviour, is likely influenced by prior learning experiences, as many dog owners train their puppies to lift their paws (Wells et al., 2018). Consequently, the use of either the left or right paw may have been unintentionally reinforced during this training. For complete studies and designs, see Table 3.

Table 3

A list of Studies Illustrating the Development of the Design of the Paw-lifting Test.

Publications	Method	Data collection	Data analysis
Wells (2003)	At the experimenter's command, the dog was instructed to sit and raise a paw. To prevent any bias in paw preference due to uneven weight distribution on the hindquarters, the dog was positioned symmetrically before the command to lift a paw was issued.	The first paw the dog lifted was recorded. 100 data points were collected for each dog.	Binomial z-scores were calculated, but the formula used was not mentioned. HI was calculated using the formula HI = (L – R/L + R).

Wells et al. (2018)	Followed the same procedure described by Wells (2003)	Same as Wells (2003). 100 data points were reduced to 50 data points because of findings on other tests	The same analysis as Wells (2003). The absolute value of LI was calculated.

6.3.1.4. The First Stepping Test

According to Tomkins and colleagues (2010b), paw preference in the first-stepping test is determined by the first paw a dog uses when going downstairs. An assistant is required to be present beside the dog to control the leash. This study compared the First-Stepping Test with the Kong ball Test and showed that the results of the first-stepping test showed greater lateralization than the Kong Ball Test (Tomkins et al., 2010b). However, the involvement of a human assistant in the procedure can introduce potential confounding variables. Therefore, a new paradigm known as the detour test has been suggested. The Detour Test introduced a task where the dog is required to travel through a transparent V-fence (Siniscalchi et al., 2013, 2016). It has been proposed as a substitute for the first-stepping test due to its capacity to assess the first paw performed by the dog without any human assistance. Considering the detour test as a novel paradigm for motor lateralization, there is a lack of research investigating the connection between the detour task and motor lateralization. Only one study has proposed that the detour task is an equally valid measure of motor lateralization compared to the first-stepping test (Plueckhahn, 2022). For complete studies and designs, see Table 4.

Table 4

A list of Studies Illustrating the Development of the Design of the First-stepping Test.

Publications	Method	Data collection	Data analysis
Tomkins et al. (2010)	The test took place on a wooden three-step staircase enclosed on both sides. Each step measured 0.16 m in height, 0.26 m in depth, and 1.5 m in width. Handrails, 1.0 m high and 3.1 m long with 0.09 m posts spaced 0.07 m apart, were present on both sides. The assistant stood beside the dog at the top of the staircase while the researchers positioned themselves about 2 meters away on the concrete base level, facing the assistant and the dog.	The initial foot the dog used to step off from a standing position was recorded 50 times.	The laterality index was calculated using the formula $LI = \frac{R-L}{R+L} \times 100$ The absolute value of LI was calculated to determine the strength of the bias. Binomial z-scores were calculated using the formula $Z = (R - [(R + L)/2)]/\sqrt{}[(R + L)/4]$
Wells et al. (2018)	Followed the same procedure described by Tomkins et al. (2010).	Same as Tomkins et al. (2010), the initial foot the dog used to step off from a standing position was recorded 50 times.	Binomial z-scores were calculated, but the formula used was not mentioned. The laterality index was calculated using the formula $HI = (L - R/L + R)$ A one-sample t-test was conducted.
Simon et al. (2022)	The test determined paw preference by	Since each start position was tested	The laterality index was calculated

	considering which front paw the dog first used to begin walking from a standing, sitting, or lying position. The dog's body needed to be evenly and symmetrically aligned in each stationary start position, with a straight spine and parallel front and hind limbs. Once the dog was positioned correctly, the owner squatted about 2 meters directly in front of the dog. The owner then called the dog and recorded which paw the dog lifted first to begin walking.	in 5 separate trials, a total of 15 data points were collected from each dog.	using the formula LI = (L – R/L + R) The absolute value of LI was calculated.

Similar to human studies, it is widely agreed that to explore the relationships between lateralization and various brain functions, careful consideration must be given to the selection of one or more research paradigms. Therefore, scientists are dedicated to evaluating different paradigms. Tomkins and his colleagues (2010a) comprehensively analyzed existing research on motor laterality in dogs. They proposed the use of a standardized evaluation method for motor laterality, specifically recommending the use of the Kong ball and the first-stepping test

(Tomkins et al., 2010b). Following that, Wells (2018) conducted an assessment of four research paradigms (the tape, the Kong ball, the paw lift, and the first-step test). The results provided further evidence to support the earlier findings, demonstrating strong test-retest reliability for both The Kong Ball Test and The First-Stepping Test, as well as the absence of population-level asymmetries in dogs (Wells., 2018).

VII. The Current Study

The proposed study was designed to evaluate three functional measures of pawedness in dogs to see which, if any, of these best correlates with each other and whether general pawedness in dogs on either an individual or population level could be identified. In this study, data on pawedness was collected through the Kong Ball Test, the V-fence Test, and the puzzle box Test. The Kong Ball Test records the paw used by the dog to stabilize the Kong ball. The V-Fence Test was designed to measure time spent on solving spatial problems among pet dogs and working dogs in the original study. It was widely used to study visual lateralization; nonetheless, it is rarely used to measure pawedness. The V-Fence Test in this study was inspired by the detour test conducted by Siniscalchi (Siniscalchi et al., 2013) and the first-stepping Test (Tomkins et al., 2010b; Wells et al., 2018). It measures the paw used for the dog's first step and the direction the dog chooses to detour around the fence. The Puzzle Box Test records the paw used by the dog to alter the direction of the rolling ball. In addition to conducting a parallel analysis of the data, the study analyzed and compared the combined paw preferences using three paradigms.

VIII. Method

8.1. Data Source

The dataset shown in video format originated from a comprehensive project conducted in 2015 and 2016 by Dr. Karen Overall, that aims to compare different task performances between pet dogs and working dogs. The task varieties and the focus on cognitive abilities in the original study provide the potential for reusing the data to look into paw preferences across dogs. Based on the focus of the current study, three specific tests have been selected from original videotapes, namely the Kong Ball Test, the V-fence test, and the puzzle box test, for their potential to exhibit paw preferences.

8.2. Subjects

There were 144 dogs, and their owners in North America participated in the original study. The whole study took place at a veterinary teaching clinic. Owners were given information about the study and completed a questionnaire that included demographic information after the test. Due to the time gap between the original study and the current study, some of the raw data is incomplete. Based on the review of all existing data, 71 dogs missing videos, questionnaires or both were excluded from this study. Additionally, 23 dogs who failed to complete at least one of the three tests were excluded. A special case involved a dog who had lost one of its paws; considering potential issues with balance and compensatory behaviours, the dog was also excluded from the analysis. While organizing the data, one dog's footage file name (Shiner) was found to be exchanged with another dog (Passion); after switching them back, Shiner's data was included, but Passion's data was excluded due to the missing camera angle.

Thus, 40 dogs' data were considered valid and used in this study, including 20 males and 20 females, with 80% of dogs being neutered or spayed. Furthermore, breeds are widespread from large dogs to small dogs, including 11 Labrador Retrievers, 9 Border Collies, 5 Mixed breeds, 3 Golden Retrievers, 2 Australian Cattle Dogs, and 1 of each following breed:

Doberman, Belgian Sheepdog, Pit Bull, Borzoi, Bearded Collie, American Cocker Spaniel, German Shepherd, Portuguese Water Dog, and Shetland Sheepdog. With the given information in the questionnaires, 17.5% of dogs had previous experience with the Kong ball, 50% of dogs had no Kong ball experience before, and 32.5% of the dogs were unknown. The assessment of the demographic information from questionnaires confirmed that all 40 dogs that has been used in the present study were companion dogs rather than working dogs.

8.3. Materials And Procedure

The whole procedure was recorded from two camera angles. Camera 1 was positioned in the right corner in front of the room, while camera two was positioned in the middle at the end of the room. Both were mounted on a tripod. Camera 1 stayed stationary most of the time but was held by one of the researchers in the Kong Ball Test to track behaviours. Camera 2 remained stationary throughout the whole recording (See Figures 4.1 and 4.1).

Figure 4.1

The Position of Camera 1

Picture removed due to proprietary issues

Note. Screenshot from selected video.

Figure 4.2

The position of Camera 2

Picture removed due to proprietary issues

Note. Screenshot from selected video.

8.3.1. Kong Ball Test

The original purpose of the Kong Ball Test was to analyze the change of facial and tongue expressions under stimuli that could cause unpleasant emotions. Two different Kongs were provided to the dog, one filled with peanut butter and the other with yogurt, to match different food preferences; dogs were allowed to freely interact with either Kong, with their owner sitting on a chair near the Kong. The chair and Kongs are placed in the center of a long rectangular black yoga mat, and the test is 5 minutes for each dog (See Figure 5). During the test, dogs were exposed to different sounds, including rain, thunder, fireworks, gunshots, and explosions, and the speaker played the sounds. The owner was not allowed to give the dog oral or physical encouragement. During the test, the dog's stress level was assessed by the original researcher, a veterinarian. The test ended immediately for the dog who showed severe stressful behaviours, such as crawling on the owner’s knees or hiding under the chair. The behaviour recorded in the Kong Ball Test is considered the paw used to stabilize the Kong, which is also used in the study conducted by Wells (Wells et al., 2017). Paw use is placing one or both paws on the Kong ball. A new paw-use behaviour was recorded each time the animal removed its paw from the Kong and placed one or both paws back on it. When the dog places both paws on the Kong ball, this behaviour is recorded, and this data point indicates a lack of paw preference. Additionally, the percentage of time each dog spent using their left or right paw to stabilize the Kong ball was also recorded.

Figure 5

The Setup for the Kong Ball Test

Picture removed due to proprietary issues

Note. Screenshot from selected video.

8.3.2. The V-Fence Test

Dogs were placed at a starting point with their owner and asked to navigate around a V-shaped transparent fence to get the Kong that contained food on the other side (See Figure 6).

The whole process included six trials, divided into two sets of 3 trials each. In the first set, the subject starts from the apex of the V-Fence and navigates towards the Kong. The starting point and the Kong positions were reversed in the second set. Furthermore, the order of the first and the second set was assigned randomly to different dogs to control the order effects. The paw use recorded for each trial is considered the first paw used to initiate movement and the direction of travel.

Figure 6

The Setup for the V-Fence Test

Picture removed due to proprietary issues

Note. Screenshot from selected video.

8.3.3. The Puzzle Box Test

The Puzzle Box Test was originally designed to assess the problem-solving ability of pet dogs and working dogs. The Puzzle Box was a semi-transparent rectangular box with nine open holes on top of it. It had two sizes that fit large and small dogs (See Figures 7.1 and 7.2). Dogs were asked to get the tennis ball from any of the nine holes on the box within 5-minutes.

However, due to different motivations and reactions to the tennis ball among individual dogs, the Kong ball was introduced as an alternative for dogs that showed no interest in the tennis ball. The behaviours used to observe paw uses are reaching, stepping, and scratching/digging. Reaching was defined as putting the right or left paw into the hole to contact the ball. The paw use in the stepping behaviour was defined as the initial use of the left or right paw to begin stepping onto the box. Scratching/digging behaviour was defined as using paws to scrape or dig repeatedly at the box's surface or the floor adjacent to the box. If the dog used the left and right paw alternately, this data point was considered as use of both paws and indicated a lack of paw preference.

Figure 7.1

The Setup of Puzzle Box for Large Dogs

Picture removed due to proprietary issues

Note. Screenshot from selected video.

Figure 7.2

The Setup of Puzzle Box for Small Dogs

Picture removed due to proprietary issues

Note. Screenshot from selected video.

8.4. Data Analysis

Manual analysis of the video tapes was augmented using the Behavioral Observation Research Interactive Software (BORIS). The software annotated and coded the behaviours based on a predefined repertoire. The raw footage was imported into BORIS for detailed analysis. BORIS allows the synchronization of starting points by adjusting the offset of each video, allowing you to watch two or more recorded videos simultaneously (See Figure 8.1). Therefore, videos that were taken from two cameras were synchronized and examined at the same time. Once the video coding was completed, a behavioural time budget was analyzed by selecting the specific observation (See Figure 8.2). To ensure reliability, the observer was trained to use the coding scheme in BORIS properly before the data collection.

Figure 8.1

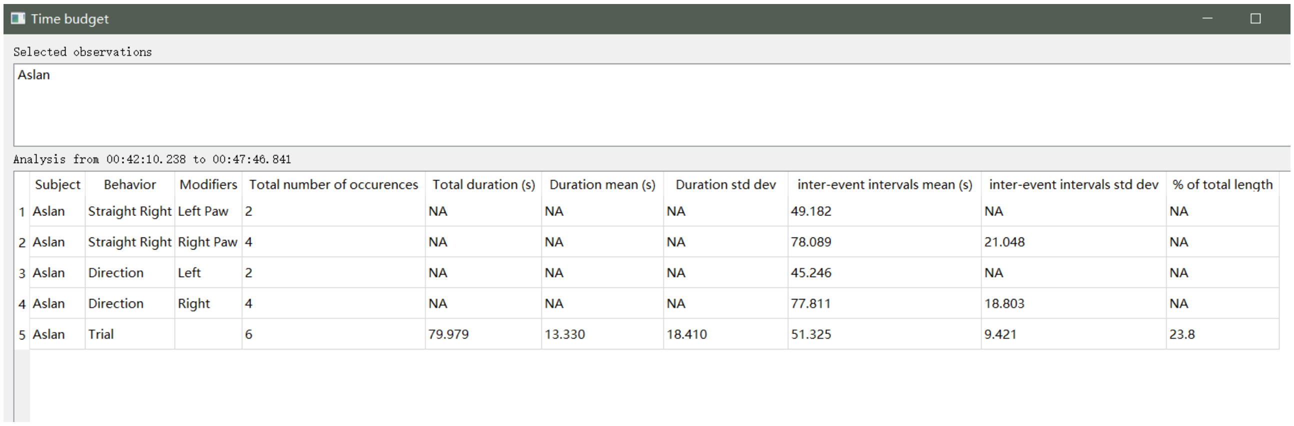
Examples of BORIS When the Video was Coded

Picture removed due to proprietary issues

Note. Screenshot from BORIS on selected video.

Figure 8.2

Examples of the Time Budget



Selected observations

Aslan

Analysis from 00:42:10.238 to 00:47:46.841

	Subject	Behavior	Modifiers	Total number of occurences	Total duration (s)	Duration mean (s)	Duration std dev	inter-event intervals mean (s)	inter-event intervals std dev	% of total length
1	Aslan	Straight Right	Left Paw	2	NA	NA	NA	49.182	NA	NA
2	Aslan	Straight Right	Right Paw	4	NA	NA	NA	78.089	21.048	NA
3	Aslan	Direction	Left	2	NA	NA	NA	45.246	NA	NA
4	Aslan	Direction	Right	4	NA	NA	NA	77.811	18.803	NA
5	Aslan	Trial		6	79.979	13.330	18.410	51.325	9.421	23.8

Note. Screenshot from BORIS showing the time budget.

The data points collected from the three tasks were converted into percentages to represent the proportion of paw used for each task. In the Kong Ball Test, the percentage of time each dog spent using their left or right paw to stabilize the Kong was considered. In the V-Fence Test, given that each trial can only observe one paw use and one direction choice, the percentage of left or right paw use was considered to be converted out of 6 trials. The Puzzle Box Test considered the percentage of time each dog spent using their paws to dig around the box. This approach was necessary because the tasks were not originally designed to measure pawedness, leading to inconsistency in data attributes. For instance, instead of ending the task after collecting 50 data points of paw use in the Kong Ball Test, a 5-minute timeframe was used for task completion. Following Tomkins' recommendation of a minimum of 45 data points (Tomkins et al., 2010a), only four dogs achieved this in the Kong Ball Test, which is insufficient for group-level analysis. Therefore, the independent variables in this study were the three tasks and the total time the dog spent on each task. The dependent variables were the proportion of time spent using the left paw and the right paw.

For each test, the LI is calculated using the formula to indicate the individual's pawedness for each behaviour.

$$Laterality\ Index\ (LI) = \frac{\text{Proportion of time spent using the right paw} - \text{Proportion of time spent using the left paw}}{\text{Proportion of time spent using the right paw} + \text{Proportion of time spent using the left paw}}$$

This formula of LI was adapted by Demirbas and her colleagues (Demirbas et al., 2023), which is $LI = \frac{Right\ paw\ use - Left\ paw\ use}{Right\ paw\ use + Left\ paw\ use}$, The right and left paw use represents the number of right and left paw use. The laterality index (LI) ranges from −1.0 to +1.0, with 1.0 indicating only the use of the right paw and -1.0 indicating only the use of the left paw. Additionally, the absolute value of the LI determines the strength of lateralization. A one-sample t-test was conducted subsequently using the absolute value of the LI to explore the population level of lateralization regardless of direction.

Second, following the procedures of Demirbas et al., 2023, binomial Z-scores were calculated for each dog using the formula to determine whether dogs exhibited a significant bias in paw preference at the individual level. $z = \frac{R-0.5N}{\sqrt{0.25N}}$. In this formula, N represents the total number of paw use, and R represents the number of right paw use. Based on the Z-scores, dogs with $z \geq 1.96$ were classified as right-pawed (R-pawed), while those with $z \leq -1.96$ were classified as left-pawed (L-pawed) (Demirbas et al., 2023). Dogs with Z-scores between +1.96 and -1.96 were considered to show no evidence of lateralization. Meanwhile, to analyze the three tasks comprehensively, a correlation test is conducted for all the behaviours in the three tasks.

IX. Results

9.1. Distribution of Pawedness

9.1.1. Kong Ball Test

The individual paw preferences for each dog in the Kong Ball Test were presented in Table 7. According to Z-scores, the number of paw use showed that only 2 (5%) of the dogs were right-pawed, 2 (5%) were left-pawed, and 36 (90%) exhibited no evidence of paw preference. However, the time each dog spent using their left or right paw revealed that 11 (27.5%) of the dogs were right-pawed, 5 (12.5%) were left-pawed, and 24 (60%) demonstrated no evidence of paw preference. The mean LI was 0.067 (± 0.472) for the number of paw use and 0.096 (± 0.590) for the percentage of time. A one-sample t-test on the absolute value of the LI for both the number and percentage of times a paw was used during the Kong test revealed that it was significantly different from zero (*t* [39] = 8.446, *p* < .001; *t* [39] = 6.602, *p* < .001, respectively), indicating that there was a strong paw preference regardless of direction.

Table 6

The individual Paw Preferences for Dogs in Kong Ball Test and V-Fence Test.

Subjects	Kong Ball		V-Fence	
	Number	Percentage of time	Number	Direction
Aili	NE	NE	NE	R
Alba	NE	NE	R	R
Aslan	NE	R	NE	NE
Bella	NE	R	NE	NE
Bing	NE	R	NE	NE
Bowser	NE	R	NE	NE
Caeli	NE	NE	NE	NE
Cleo	NE	NE	NE	NE
Edy	NE	NE	NE	NE
Flurry	NE	NE	L	L
Giddyup	NE	NE	NE	NE
Haka	NE	NE	NE	NE
Hannah	NE	NE	NE	NE
Honky Tonk	NE	NE	NE	NE
Jess	NE	NE	NE	NE
Josie	NE	R	NE	NE
Kali	NE	L	NE	NE
Keeley	NE	R	NE	R
Kiri	NE	NE	NE	NE
Kiva	NE	NE	NE	R
Ludo	NE	R	NE	NE
Luigi	R	R	NE	NE
Noah	NE	NE	NE	L
Paden	NE	NE	NE	NE
Party	NE	NE	NE	NE
Shiner	NE	L	NE	NE
Ranger	L	L	L	L
Rhys	NE	R	NE	NE
Ricky	NE	NE	NE	R
Sadie	R	R	NE	NE

Shea	NE	NE	NE	L
Shiloh	NE	NE	NE	NE
Sky	NE	R	NE	R
Sophie	L	L	L	NE
Stella	NE	NE	NE	NE
Striker	NE	NE	NE	NE
Sunny	NE	NE	NE	NE
Trevi	NE	NE	NE	NE
Wilbur	NE	NE	NE	R
Zephryr	NE	L	NE	NE

Note. “R”= Right pawed, “L” = Left pawed, “NE” = No Evidence. For a complete table including LI and z-scores, see Appendix A and B.

9.1.2. V-Fence Test

The individual paw preferences for each dog in the V-Fence Test were presented in Table 5. According to z-scores, the number of paw use showed that only 1 (2.5%) of the dogs were right-pawed, 3 (7.5%) were left-pawed, and 36 (90%) exhibited no evidence of paw preference. Additionally, the direction of V-Fence each dog chose revealed that 7 (17.5%) of the dogs were right-pawed, 4 (10%) were left-pawed, and 29 (72.5%) demonstrated no evidence of paw preference. The mean LI was -0.025 (± 0.491) for the number of paw use and 0.160 (±0.646) for the direction of V-Fence. A one-sample t-test on the absolute value of the LI for both the first step in the V-Fence task and its direction revealed that it was significantly different from zero (t [39] = 7.575, $p < .001$; t [39] = 9.731, $p < .001$, respectively), indicating that there was a strong paw preference regardless of direction.

9.1.3. Puzzle Box Test

The individual paw preferences for each dog in the Puzzle Box Test were presented in Table 6. According to z-scores, the time each dog spent using their left or right paw to dig showed that only 1 (2.5%) of the dogs were right-pawed, 4 (10%) were left-pawed, and 35 (87.5%) exhibited no evidence of paw preference. Additionally, the stepping behaviour did not reveal any paw preferences. Similarly, the number of paws used to reach the ball revealed no right-pawed dog; only 1 (2.5%) showed left-pawed, and 39 (97.5%) dogs demonstrated no paw preference. The analysis of both data for stepping and paw reaching showed that there were only 1 (2.5%) right-pawed, 2 (5.0%) left-pawed, and 37 (92.5%) showed no evidence of paw preference. The mean LI was -0.115 (± 0.652) for the digging behaviour, and for the stepping and paw reaching was -0.130 (±0.594) and 0.003 (±0.544), respectively. The mean LI for stepping and paw reaching was -0.019 (±0.606). A one-sample t-test on the absolute value of the LI for the Puzzle Box Test, revealed that both the reaching and stepping tasks were significantly different from zero (t (39) = 4.86, p < .001; t (39) = 5.84, p < .001), as well as when these tasks were combined (t (39) = 6.73, p < .001). However, the absolute LI for scratching and digging did not reach significance (t (39) = -1.12, p = 0.271), indicating a lack of paw preference regardless of direction.

Table 7

The individual Paw Preferences for Dogs in Puzzle Box Test.

Subjects	Puzzle Box Test			
	Digging (%)	Stepping (S, #)	Reaching (R, #)	S+R
Aili	NE	NE	NE	NE
Alba	NE	NE	NE	NE
Aslan	NE	NE	NE	NE
Bella	NE	NE	NE	NE
Bing	NE	NE	NE	NE
Bowser	L	NE	NE	NE
Caeli	NE	NE	L	L
Cleo	R	NE	NE	NE

Edy	NE	NE	NE	NE
Flurry	NE	NE	NE	NE
Giddyup	NE	NE	NE	L
Haka	NE	NE	NE	NE
Hannah	NE	NE	NE	NE
Honky Tonk	NE	NE	NE	NE
Jess	NE	NE	NE	NE
Josie	NE	NE	NE	NE
Kali	L	NE	NE	NE
Keeley	NE	NE	NE	NE
Kiri	NE	NE	NE	NE
Kiva	NE	NE	NE	NE
Ludo	NE	NE	NE	R
Luigi	L	NE	NE	NE
Noah	NE	NE	NE	NE
Paden	NE	NE	NE	NE
Party	NE	NE	NE	NE
Shiner	NE	NE	NE	NE
Ranger	NE	NE	NE	NE
Rhys	NE	NE	NE	NE
Ricky	NE	NE	NE	NE
Sadie	NE	NE	NE	NE
Shea	L	NE	NE	NE
Shiloh	NE	NE	NE	NE
Sky	NE	NE	NE	NE
Sophie	NE	NE	NE	NE
Stella	NE	NE	NE	NE
Striker	NE	NE	NE	NE
Sunny	NE	NE	NE	NE
Trevi	NE	NE	NE	NE
Wilbur	NE	NE	NE	NE
Zephryr	NE	NE	NE	NE

Note. “R”= Right pawed, “L” = Left pawed, “NE” = No Evidence. For a complete table including LI and z-scores, see Appendix C.

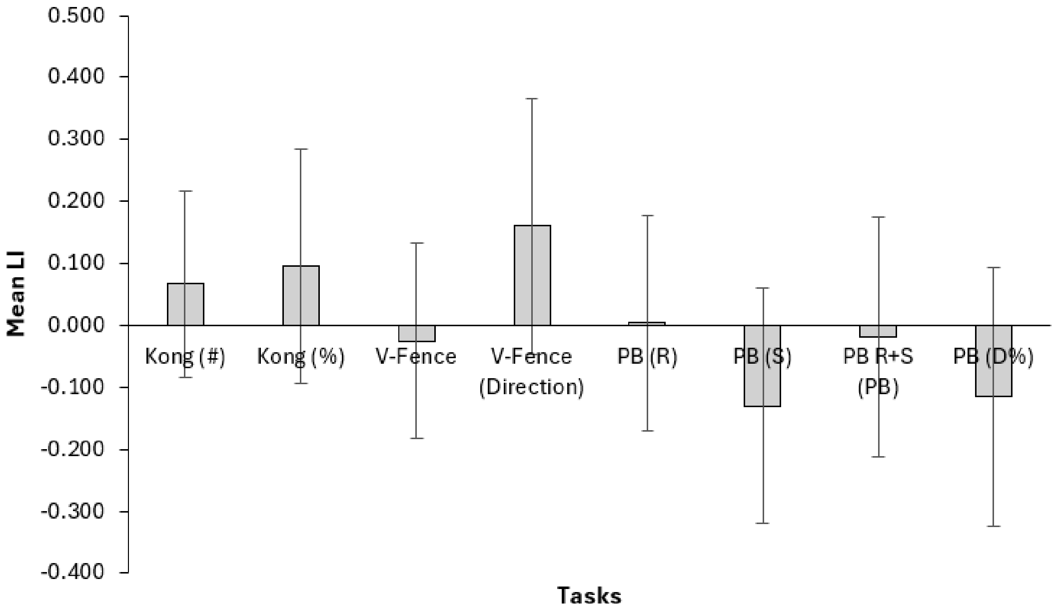
9.2. Direction and Strength of Lateralization Among Three Tasks

9.2.1. Significance Test

Although the analysis of the mean laterality index (LI) across all tasks seemed to reveal a tendency toward either right-pawed or left-pawed preferences, the analysis with 95% confidence intervals across all tasks indicated no significant population-level lateralization (see Figure 9.1). Furthermore, almost all tasks exhibited wide error bars with standard deviation, which further demonstrated that while some dogs exhibited strong lateralization, this effect was inconsistent across the population (see Figure 9.2).

Figure 9.1

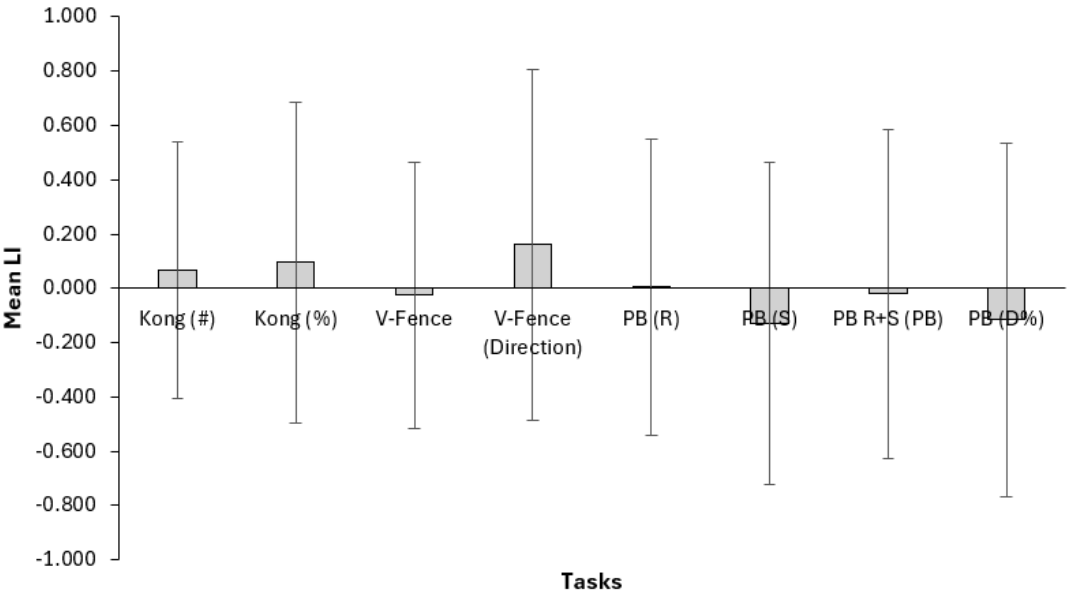
Mean Laterality Index (LI) with 95% Confidence Intervals Across Various Tasks.



Note. Error bars represent the 95% Confidence Intervals. The mean LI values indicate varying degrees of lateralization across tasks, with some tasks showing potential lateralization while others do not. Tasks, where the error bars cross zero, suggest no significant lateralization at the population level.

Figure 9.2

Mean Laterality Index (LI) with Standard Deviation Error Bars Across Various Tasks.



Note. Error bars represent the standard deviations. The wide error bars across most tasks indicate high variability in paw preference within the population, suggesting significant individual differences in lateralization.

9.2.2. Correlation Test

Table 7 shows the correlations among different tasks. The test results indicated a significant positive correlation between the LI for the number and percentage of times a paw was used during the Kong Test ($r = 0.709$, $p < .001$), indicating that the frequency of paw use was closely aligned with the proportion of paw use in this task. Interestingly, there was a moderate positive correlation between the LI for the number of paws used as the first step in the V-Fence Test and the percentage of times a paw was used in the Kong Ball Test ($r = 0.373$, $p < .05$). This suggested that the paw chosen for the initial step in the V-Fence Test was associated with the proportion of paw use in the Kong Ball Test. Additionally, the LI for the direction in the V-Fence Test was significantly correlated with the number of paws used as the first step in the V-Fence Test ($r = 0.406$, $p < .01$). The LI in the Reaching and Stepping tasks of the Puzzle Box Test were significantly correlated with the combination of both tasks ($r = 0.585$, $p < .001$; $r = 0.566$, $p < .001$, respectively). Interestingly, the digging task showed a significant correlation with the stepping task ($r = 0.365$, $p < .05$), as well as with the combined data of the reaching and stepping tasks ($r = 0.378$, $p < .05$). This suggested that the frequency of paw use for digging or scratching was related to the paw chosen for initiating stepping and reaching.

Table 8

Correlation between different tasks for LI.

	Kong (%)	VF (#)	PB Digging	PB (R+S)
Kong (#)	0.709***			
VF (#)	0.373*			
VF Direction		0.406**		
PB (R+S)			0.378*	
PB (Stepping)			0.365*	0.585***
PB (Reaching)				0.566***

Note. Numbers indicate correlation coefficients, see Appendix D for the full correlation table. Asterisks indicate p-values with * $p < .05$, ** $p < .01$, *** $p < .001$

X. Discussion

This study used the Kong Ball, V-Fence, and Puzzle Box tests to explore canine laterality, focusing on various tasks to gather paw usage data. Previous research on this topic yielded results regarding individual levels of lateralization in canines. Most studies have reported a high percentage of lateralized individuals, leading to the conclusion that, unlike humans, dogs do not exhibit population-level lateralization but rather individual level (Tan, 1987; Wells, 2003; Branson & Rogers, 2006; Siniscalchi et al., 2008). The results of this study seem to be contradicted by previous studies, as dogs in this study did not exhibit individual-level asymmetry across all tests. In fact, other non-human animals, such as cats, horses, and birds, also show individual-level asymmetry without consistent population-level lateralization (Demirbas et al., 2019).

In the present study, the LI and the binomial z-scores analysis indicated that the dogs tested did not exhibit lateralization at the group level. While this finding did not align with most existing literature, some studies found results similar to the current study (Demirbas et al., 2023; McGreevy et al., 2010). According to Demirbas et al. (2023), increased acute stress levels can interfere with the expression of lateralization and increase ambilateral behaviours, which may explain the results of this study. Since this study occurred at a veterinary teaching clinic, the dogs tested were likely exposed to potential stress-inducing factors. For example, the dogs may have been exposed to the odour of veterinary sweat or the nervous barking of other dogs. Furthermore, the Kong Ball Test was originally designed to examine facial and tongue expressions under stress, so all the dogs were exposed to a series of sounds that could have heightened their stress levels.

When explaining the results from the Kong Ball Test, it is necessary to consider that the idea of using the Kong Ball Test as a measure of lateralization comes from assumptions drawn from human studies. As discussed in the introduction, the non-dominant hand in humans is typically used for stabilizing tasks and corrective movements, while the dominant hand is reserved for tasks requiring greater precision. This finding could also be applied to canines. Wells and colleagues (2016) compared the limb preferences of canines and humans on the Kong Ball Test and hypothesized that dogs might have used their non-dominant paw for stabilization while leaving the dominant paw for postural support or tasks requiring more motor control. However, it is also well-discussed that the tasks that require greater precision in humans are generally considered to be finger control, such as finger-tapping. Dogs, on the other hand, did not have the ability to control the fingers separately. Therefore, in this study, the paw used to stabilize the Kong the most is considered the dominant paw as the majority of studies used this definition.

Another factor that may have influenced the results was the limitation in the number of data points. Tomkins and colleagues (2010a) suggested that at least 45 data points per subject are necessary for reliable observation of pawedness. However, because the tests used in this study were not specifically designed to measure pawedness, there was insufficient data collection. This lack of data could also explain why no group-level lateralization was observed. Despite the absence of a clear population-level trend, the results of the one-sample t-test on the strength of the LI indicated that individual dogs did exhibit paw preferences, whether right or left. This suggests that paw preferences existed among individual dogs but were inconsistent across the population.

As previously mentioned, most existing literature on canine laterality employed various methodologies but usually focused on a single test within one study. Since dogs and humans share several basic behavioural and functional characteristics, one could argue that combining different tests and analyzing the results might provide a more reliable approach to exploring lateralization than focusing on a single test.

The correlation analysis identified relationships within and across different tasks in this study. The results indicated that the frequency of paw use was strongly correlated with the proportion of paw use within the Kong Ball Test, suggesting a consistent lateralization pattern during this task. Additionally, a significant correlation was observed between the direction chosen and the first step taken in the V-Fence Test. This finding underscores the link between the initial paw used and the directional choice in the V-Fence Test, indicating a coherent lateralization pattern within this specific task. This observed pattern may be attributed to the dog's innate tendency to favour one side of its body when making directional decisions.

Furthermore, the correlations identified between the digging task, the stepping task, and the combined reaching and stepping tasks within the Puzzle Box Test suggest that the paw used for digging or scratching is related to the paw selected for initiating other motor activities, such as stepping and reaching. Prior research has established that lateralization in motor tasks is often associated with brain hemisphere dominance. This could account for the consistent preference for certain paws in tasks requiring similar motor skills, such as digging, stepping, and reaching (Rogers, 2010b).

This study also observed a positive correlation between the Kong Ball Test and the V-Fence Test but not with the Puzzle Box Test. The link was found specifically between the LI for the first step in the V-Fence Test and the percentage of times a paw was used in the Kong Ball Test. This finding suggested a relationship between the paw used to initiate movement in the V-Fence Test and its usage frequency in the Kong Ball Test, potentially indicating a generalization of lateralization tendencies across different tasks.

However, it was important to consider the order in which the dogs were tested. The Puzzle Box Test was administered first, followed by the V-Fence Test, and finally, the Kong Ball Test.

The observed correlation between the V-Fence Test and the Kong Ball Test might be attributed to the reinforcement of a paw preference through rewards in the earlier tasks, which could have subsequently influenced the dogs' choices in later tasks involving similar motor actions. Additionally, the complexity of the tasks should be taken into account as well. As discussed, the association between limb preference and task complexity has already been demonstrated in humans and primates. In canine studies, the variations in the tasks used to assess pawedness often appeared together with differences in the reported preferences (Wells, 2003; Poyser et al., 2006; Batt et al., 2008; Tomkins et al., 2010b). As a result, it is reasonable to hypothesize that the association between limb preference and task complexity could be generalized in canines. Therefore, the absence of correlation between the Puzzle Box Test and either the Kong Ball Test or V-Fence Test may be attributed to the variation in task complexity.

Moreover, there has been contradictory discussion regarding the validity of the Kong Ball Test, particularly concerning the random manner in which dogs stabilize the Kong (Isparta et al., 2024; Wells et al., 2016; Wells, 2021). Additionally, researchers had proposed that the asymmetrical design of the Kong, with one hole being larger than the other, might pose a disadvantage (Wells., 2016; Isparta et al., 2024). This design feature could lead dogs to focus primarily on accessing food through the larger hole, thereby limiting the accuracy of measuring lateralization.

XI. Conclusion

Overall, the current study did not find any lateralization towards left or right for pawedness on a group level but found supporting evidence for pawedness regardless of direction. The study also found correlations between the Kong ball and the V-Fence Test, which might indicate a potential for generalization among different methodologies in the future. However, the results of this study could be influenced by limitations on test designs, stress levels, and the number of data points collected. Additionally, previous studies have identified a connection between sex and laterality index (LI) (McGreevy et al., 2010; Ocklenburg et al., 2019), as well as a relationship between initial paw use and overall paw preference in dogs (Demirbas et al., 2023). However, these associations were not explored in this study.

Recent literature by Isparta and colleagues (2024) introduced a new paradigm called the food-reaching test (FRT), which has been proposed as a more effective method than the Kong Ball Test. The FRT is considered advantageous due to its standardized nature and the higher level of engagement observed among dogs, with more dogs showing interest in the FRT compared to the Kong Ball Test (Demirbas et al., 2023). Although the study reported no significant correlation between Kong Ball Test and FRT, this finding underscores the need for further investigation. Future research should continue exploring new methodologies and potentially integrating different approaches. This will determine if there are consistent patterns or generalizable findings across various testing paradigms in canine lateralization studies.

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Appendix A

The Individual Paw Preferences for Dogs in the Kong Ball Test

Subject	Kong ball					
	Number			Percentage of time		
	LI	Z-score	Pref	LI	Z-score	Pref
Aili	0.00	0.00	NE	0.00	0.00	NE
Alba	-0.25	-0.71	NE	0.15	0.88	NE
Aslan	0.56	1.67	NE	0.71	2.13	R
Bella	-0.22	-0.94	NE	0.44	2.59	R
Bing	1.00	1.41	NE	1.00	5.76	R
Bowser	0.00	0.00	NE	0.74	4.37	R
Caeli	0.00	0.00	NE	0.00	0.00	NE
Cleo	-0.50	-1.00	NE	0.72	1.82	NE
Edy	0.00	0.00	NE	0.00	0.00	NE
Flurry	0.33	0.58	NE	-0.58	-1.21	NE
Giddyup	-0.07	-0.26	NE	0.21	1.41	NE
Haka	0.60	1.34	NE	0.03	0.05	NE
Hannah	0.00	0.00	NE	-0.32	-1.51	NE
Honky Tonk	0.09	0.52	NE	0.17	1.39	NE
Jess	-0.50	-1.00	NE	-0.45	-1.60	NE
Josie	0.12	0.60	NE	0.68	5.99	R
Kali	-0.43	-1.60	NE	-0.67	-2.68	L
Keeley	1.00	1.41	NE	1.00	2.32	R
Kiri	0.00	0.00	NE	0.00	0.00	NE
Kiva	0.50	1.00	NE	0.90	1.85	NE
Ludo	0.50	1.41	NE	0.35	2.55	R
Luigi	0.78	4.04	R	0.88	4.48	R
Noah	-0.25	-1.00	NE	-0.02	-0.11	NE

Paden	-1.00	-1.41	NE	-1.00	-1.14	NE
Party	-0.33	-0.58	NE	-0.62	-1.27	NE
Shiner	0.00	0.00	NE	-0.38	-2.73	L
Ranger	-0.37	-2.34	L	-0.65	-3.16	L
Rhys	0.50	1.00	NE	0.95	3.93	R
Ricky	0.20	0.63	NE	-0.29	-1.31	NE
Sadie	1.00	2.65	R	1.00	6.98	R
Shea	-0.33	-0.58	NE	0.23	0.26	NE
Shiloh	-0.06	-0.34	NE	0.18	1.32	NE
Sky	0.71	1.89	NE	0.92	4.51	R
Sophie	-0.87	-3.36	L	-0.88	-4.91	L
Stella	-0.33	-0.58	NE	-0.25	-0.22	NE
Striker	0.00	0.00	NE	0.00	0.00	NE
Sunny	0.00	0.00	NE	-0.74	-1.61	NE
Trevi	0.29	1.07	NE	0.15	0.87	NE
Wilbur	0.00	0.00	NE	0.00	0.00	NE
Zephryr	0.00	0.00	NE	-0.73	-2.28	L

Note. “R” = Right pawed, “L” = Left pawed, “NE” = No Evidence.

Appendix B

The Individual Paw Preferences for Dogs in the V-Fence Test

Subject	V-Fence					
	Number			Direction		
	LI	Z-Score	Pref	LI	Z-Score	Pref
Aili	0.333	0.82	NE	1.000	2.45	R
Alba	1.000	2.45	R	1.000	2.45	R
Aslan	0.333	0.82	NE	0.333	0.82	NE
Bella	0.333	0.82	NE	0.667	1.63	NE
Bing	0.333	0.82	NE	-0.200	-0.82	NE
Bowser	0.000	0.00	NE	0.667	1.63	NE
Caeli	0.333	0.82	NE	-0.333	-0.82	NE
Cleo	-0.333	-0.82	NE	0.000	0.00	NE
Edy	-0.333	-0.82	NE	-0.667	-1.63	NE
Flurry	-1.000	-2.45	L	-1.000	-2.45	L
Giddyup	0.333	0.82	NE	0.000	0.00	NE
Haka	0.000	0.00	NE	0.333	0.82	NE
Hannah	-0.333	-0.82	NE	-0.333	-0.82	NE
Honky Tonk	0.667	1.63	NE	0.333	0.82	NE
Jess	0.000	0.00	NE	0.000	0.00	NE
Josie	-0.667	-1.63	NE	0.000	0.00	NE

Kali	0.000	0.00	NE	0.000	0.00	NE
Keeley	0.667	1.63	NE	1.000	2.45	R
Kiri	0.000	0.00	NE	0.333	0.82	NE
Kiva	-0.667	-1.63	NE	1.000	2.45	R
Ludo	0.333	0.82	NE	0.333	0.82	NE
Luigi	0.000	0.00	NE	0.000	0.00	NE
Noah	0.000	0.00	NE	-1.000	-2.45	L
Paden	-0.333	-0.82	NE	0.667	1.63	NE
Party	0.000	0.00	NE	0.667	1.63	NE
Shiner	-0.667	-1.63	NE	0.600	0.82	NE
Ranger	-1.000	-2.45	L	-1.000	-2.45	L
Rhys	0.000	0.00	NE	-0.667	-1.63	NE
Ricky	0.000	0.00	NE	1.000	2.45	R
Sadie	0.333	0.82	NE	0.667	1.63	NE
Shea	-0.333	-0.82	NE	-1.000	-2.45	L
Shiloh	-0.333	-0.82	NE	-0.667	-1.63	NE
Sky	0.333	0.82	NE	1.000	2.45	R
Sophie	-1.000	-2.45	L	-0.333	-0.82	NE
Stella	0.667	1.63	NE	-0.667	-1.63	NE
Striker	0.667	1.63	NE	0.667	1.63	NE
Sunny	-0.667	-1.63	NE	0.667	1.63	NE
Trevi	-0.333	-0.82	NE	0.000	0.00	NE

Wilbur	0.333	0.82	NE	1.000	2.45	R
Zephryr	0.000	0.00	NE	0.333	0.82	NE

Note. “R” = Right pawed, “L” = Left pawed, “NE” = No Evidence.

Appendix C

The Individual Paw Preferences for Dogs in the Puzzle Box Test

Subject	Puzzle Box											
	Digging (%)			Stepping (S, #)			Reaching (R, #)			S+R		
	LI	Z-Score	Pref	LI	Z-Score	Pref	LI	Z-Score	Pref	LI	Z-Score	Pref
Aili	0.440	1.20	NE	0.000	0.00	NE	-1.000	-1.00	NE	-0.500	-1.00	NE
Alba	0.568	1.54	NE	1.000	1.73	NE	1.000	1.73	NE	0.714	1.89	NE
Aslan	-0.200	-0.32	NE	-1.000	-1.00	NE	0.000	0.00	NE	-1.000	-1.00	NE
Bella	0.168	0.67	NE	-1.000	-1.00	NE	1.000	1.73	NE	0.500	1.00	NE
Bing	-1.000	-0.71	NE	-1.000	-1.00	NE	0.000	0.00	NE	-1.000	-1.00	NE
Bowser	-1.000	-2.47	L	-1.000	-1.00	NE	0.000	0.00	NE	-1.000	-1.00	NE
Caeli	0.059	0.19	NE	0.333	0.58	NE	-0.667	-4.00	L	-0.676	-4.11	L
Cleo	1.000	2.92	R	0.000	0.00	NE	0.500	1.00	NE	0.600	1.34	NE
Edy	0.000	0.00	NE	-0.333	-0.58	NE	-1.000	-1.41	NE	-0.600	-1.34	NE
Flurry	0.000	0.00	NE	0.500	1.00	NE	0.000	0.00	NE	1.000	1.73	NE
Giddyup	0.103	0.35	NE	-1.000	-1.00	NE	-0.360	-1.80	NE	-0.385	-1.96	L

Haka	-1.000	-1.58	NE	0.333	0.58	NE	1.000	1.41	NE	0.600	1.34	NE
Hannah	-1.000	-1.05	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Honky Tonk	-0.308	-1.58	NE	0.600	1.34	NE	0.000	0.00	NE	0.600	1.34	NE
Jess	0.714	1.89	NE	0.500	1.00	NE	0.333	0.58	NE	0.429	1.13	NE
Josie	0.049	0.14	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Kali	-1.000	-2.88	L	-1.000	-1.00	NE	0.333	0.58	NE	0.000	0.00	NE
Keeley	0.294	0.54	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Kiri	1.000	0.89	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Kiva	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Ludo	1.000	1.30	NE	0.000	0.00	NE	0.500	1.00	NE	0.750	2.12	R
Luigi	-1.000	-2.17	L	-0.143	-0.38	NE	1.000	1.00	NE	0.200	0.45	NE
Noah	-1.000	-1.14	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Paden	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Party	0.000	0.00	NE	-1.000	-1.00	NE	0.000	0.00	NE	0.000	0.00	NE
Shiner	0.000	0.00	NE	0.333	0.58	NE	0.000	0.00	NE	1.000	1.00	NE

Ranger	1.000	1.82	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Rhys	-1.000	-1.38	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Ricky	-0.029	-0.09	NE	-0.333	-0.58	NE	-1.000	-1.00	NE	-0.500	-1.00	NE
Sadie	-0.066	-0.35	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Shea	-1.000	-3.74	L	-1.000	-1.00	NE	0.000	0.00	NE	0.000	0.00	NE
Shiloh	-0.286	-1.17	NE	-1.000	-1.00	NE	1.000	1.00	NE	0.000	0.00	NE
Sky	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Sophie	-0.032	-0.10	NE	0.000	0.00	NE	-1.000	-1.00	NE	-1.000	-1.00	NE
Stella	-0.154	-0.25	NE	-1.000	-1.00	NE	0.000	0.00	NE	-1.000	-1.00	NE
Striker	-1.000	-1.00	NE	0.000	0.00	NE	-1.000	-1.41	NE	-1.000	-1.41	NE
Sunny	-1.000	-0.55	NE	0.000	0.00	NE	-0.500	-1.73	NE	-0.500	-1.73	NE
Trevi	0.500	1.45	NE	1.000	1.00	NE	0.000	0.00	NE	1.000	1.00	NE
Wilbur	-0.075	-0.27	NE	0.000	0.00	NE	0.000	0.00	NE	0.000	0.00	NE
Zephryr	0.652	0.99	NE	1.000	1.41	NE	0.000	0.00	NE	1.000	1.41	NE

Note. “R” = Right pawed, “L” = Left pawed, “NE” = No Evidence.

Appendix D

The Complete Correlation Matrix for all Tasks

		LI KB time	**LI KB Number of times**	**LI VF Time**	**LI VF Number of times**	**LI PB digging scratch**	**LI PB reaching+stepping**	**LI PB Paw reaching**	**LI VF Direction**	**PB stepping only**
LI KB time	Pearson's r	—								
	df	—								
	p-value	—								
LI KB Number of times	Pearson's r	0.709 ***	—							
	df	38	—							
	p-value	< .001	—							
LI VF Time	Pearson's r	0.373 *	0.277	—						
	df	38	38	—						
	p-value	0.018	0.084	—						
LI VF Number of times	Pearson's r	0.373 *	0.277	1.000 ***	—					
	df	38	38	38	—					
	p-value	0.018	0.084	< .001	—					

		LI KB time	**LI KB Number of times**	**LI VF Time**	**LI VF Number of times**	**LI PB digging scratch**	**LI PB reaching+stepping**	**LI PB Paw reaching**	**LI VF Direction**	**PB stepping only**
LI PB digging scratch	Pearson's r	-0.111	-0.178	-0.020	-0.020	—				
	df	38	38	38	38	—				
	p-value	0.495	0.271	0.900	0.900	—				
LI PB reaching+stepping	Pearson's r	-0.088	0.034	-0.144	-0.144	0.378 *	—			
	df	38	38	38	38	38	—			
	p-value	0.588	0.834	0.375	0.375	0.016	—			
LI PB Paw reaching	Pearson's r	0.262	0.122	0.127	0.127	0.030	0.566 ***	—		
	df	38	38	38	38	38	38	—		
	p-value	0.102	0.454	0.434	0.434	0.854	< .001	—		
LI VF Direction	Pearson's r	0.170	0.217	0.406 **	0.406 **	0.175	0.038	-0.022	—	
	df	38	38	38	38	38	38	38	—	
	p-value	0.295	0.179	0.009	0.009	0.281	0.817	0.893	—	

		LI KB time	LI KB Number of times	LI VF Time	LI VF Number of times	LI PB digging scratch	LI PB reaching+stepping	LI PB Paw reaching	LI VF Direction	PB stepping only
PB stepping only	Pearson's r	-0.180	0.055	-0.079	-0.079	0.365 *	0.585 ***	-0.012	0.144	—
	df	38	38	38	38	38	38	38	38	—
	p-value	0.266	0.738	0.629	0.629	0.021	< .001	0.940	0.375	—

Note. * p < .05, ** p < .01, *** p < .001.
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